SPATIAL AND TEMPORAL VARIATIONS IN ROCKY INTERTIDAL COMMUNITIES

by

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INTRODUCTION

Early work on the rocky intertidal zone of the Cape Peninsula was carried out largely by algologists and was concerned with listing of species (eg. Barton, 1893; Delf, 1921; Levyns, 1924) and investigation into distributional patterns (eg. Murray, 1893, cited by Stephenson, 1944). During the 1930's and 1940's the field expanded enormously both taxonomically with the extensive algal work of Papenfuss, and ecologically. Experimental work was carried out on recolonisation (Bokenham and Stephenson, 1938) and, following initial work by Bokenham and Neugebauer (1938), an understanding of some of the causes of vertical zonation in the intertidal zone was derived (Broekhuysen, 1942; Stephenson, 1943).

During this period the extensive and illuminating work on the biogeography of the South African intertidal was carried out by Stephenson and his associates at the University of Cape Town. This uniquely comprehensive work (summarized in Stephenson, 1939, 1944, 1948) serves as the basis for our present understanding of distributional patterns along this coast. Again the algologists were advanced in this field and the studies of Isaac (1937) on the algae of the west coast of the country implicated the biogeographic significance of temperature gradients. The generalised algal zonation patterns derived during this work foreshadowed to a great extent those derived by Stephenson (1939) for the biota as a whole which are still used as a model of zonation today.

Since then ecological work on the rocky intertidal shores of the Peninsula has been largely autecological (eg. work on limpets by Branch, 1971, 1975a, 1975b, 1976 and on mussels by Griffiths, 1977) or geared towards the testing of statistical methods (eg. Field and MacFarlane, 1968; Field and Robb, 1970).

With the shift towards an understanding of ecosystems in terms of energy flow and current concern over the effects of pollution further needs have arisen. Although Bright (1938) and Eyre (1939) have provided detailed descriptions of single localities in the Peninsula and Isaac (1937) has examined a number of Atlantic coast sites

in terms of algal distribution a survey of the major beach types for the whole Peninsula is lacking. Such work may be useful for the prediction of biotic conditions on unexamined beaches, and thus of pre-disaster conditions on subsequently polluted beaches. It may also be useful as a baseline study for further energetic studies. However, information of this type can fulfil these functions only if an understanding of the underlying causes of community structure is derived.

The terms "community" and "community structure" are used here in the sense defined by Menge (1976). Community is taken to mean the directly or indirectly interacting assemblage of organisms (in this case macro-organisms) occupying a particular habitat (in this instance rocky shores). Community structure entails such attributes of the community as patterns of distribution, abundance, trophic relationships and species diversity.

Community structure may be expected to be affected by both biotic and abiotic factors. Although there is currently considerable interest in biotic interactions as major forces in community structuring (eg. the work of Menge, 1976; Dayton, 1971, 1975; Paine, 1971a; Menge and Sutherland, 1976 etc.) little work has been carried out on this locally. Similarly while Stephenson (1944) and Isaac (1937) have recognised the possible importance of various abiotic factors there have not yet been any quantitative studies on the effects of interactions of major abiotic factors on rocky beach communities, beyond a semi-quantitative study in Natal by Jackson (1976).

There is a wide diversity of beach types in the Cape Peninsula and the present work was designed to examine communities on rocky shores subjected to different combinations of physical conditions. Although the often profound influence of biotic interactions is fully recognised their investigation falls beyond the scope of this work. These are however taken into account at a generalised level.

Extensive work on the effects of isolated physical factors by previous authors and consideration of local conditions indicated that the most important physical factors to be considered were temperature,

substrate and the degree of wave exposure. An examination of beaches subjected to varying conditions of these three factors provides a broad survey of intertidal conditions on rocky shores in the Cape Peninsula. It may also yield some insight into the relative importance of these factors and their interactions as revealed by community structure and trophic structure. This may then give a better understanding (on a quantitative basis) of the relative importance of trophic compartments under varying conditions. The most relevant points of interest for further energetic studies may thus be indicated and a preliminary understanding of the types of energy flow patterns may be derived.

Of course ecosystems vary temporally as well as spatially. This may be due to seasonal or longer term changes in the system. A framework describing seasonal changes under undisturbed conditions is thus required. This may provide a background for an understanding of future changes due to human interference and also form the groundwork for certain aspects of annual energy budgets.

In order to monitor some of these seasonal changes Dalebrook beach in False Bay was selected as a convenient, "typical" exposed beach where vertical zonation is clear. Seasonal changes in biomass, zonation and calorific value of the major primary producers were monitored. In addition the population size and composition of the two abundant gastropods Oxystele variegata and Littorina africana knysnaensis at Dalebrook were examined on a seasonal basis and factors influencing their zonation investigated.

This thesis thus attempts to give an understanding of intertidal conditions in the Cape Peninsula in terms of spatial and seasonal variations in rocky shore communities and falls into two distinct parts:

1. A general survey of intertidal conditions and an investigation of the interactions of certain physical factors on rocky shore communities.
2. An investigation of seasonal changes in the populations of certain abundant algae and gastropods at Dalebrook.

PART I

CHAPTER 1 : STUDY AREA AND METHODS

This section entails a survey of intertidal conditions in the Cape Peninsula including:

1. A description of vertical zonation in the Peninsula as a whole derived from the different beach types examined.

2. An examination of trophic abundance on these beaches and the relative significance of different trophic compartments.

3. An investigation into the interactions and effects of wave exposure, substrate and temperature on beach communities. This forms the main thrust of Part I and throughout this section trends in response to these factors are highlighted.

FIG. 1.1 Map of the Cape Peninsula showing the four intertidal biotic regions (A-D) recognised by Stephenson (1944) (see text). Inset shows the three intertidal provinces of South Africa (Stephenson, 1944);
1 = East coast (Upangazi to Port Edward),
2 = South coast (Port Elizabeth to Cape Agulhas),
3 = West coast (Kommetjie to Port Nolloth).

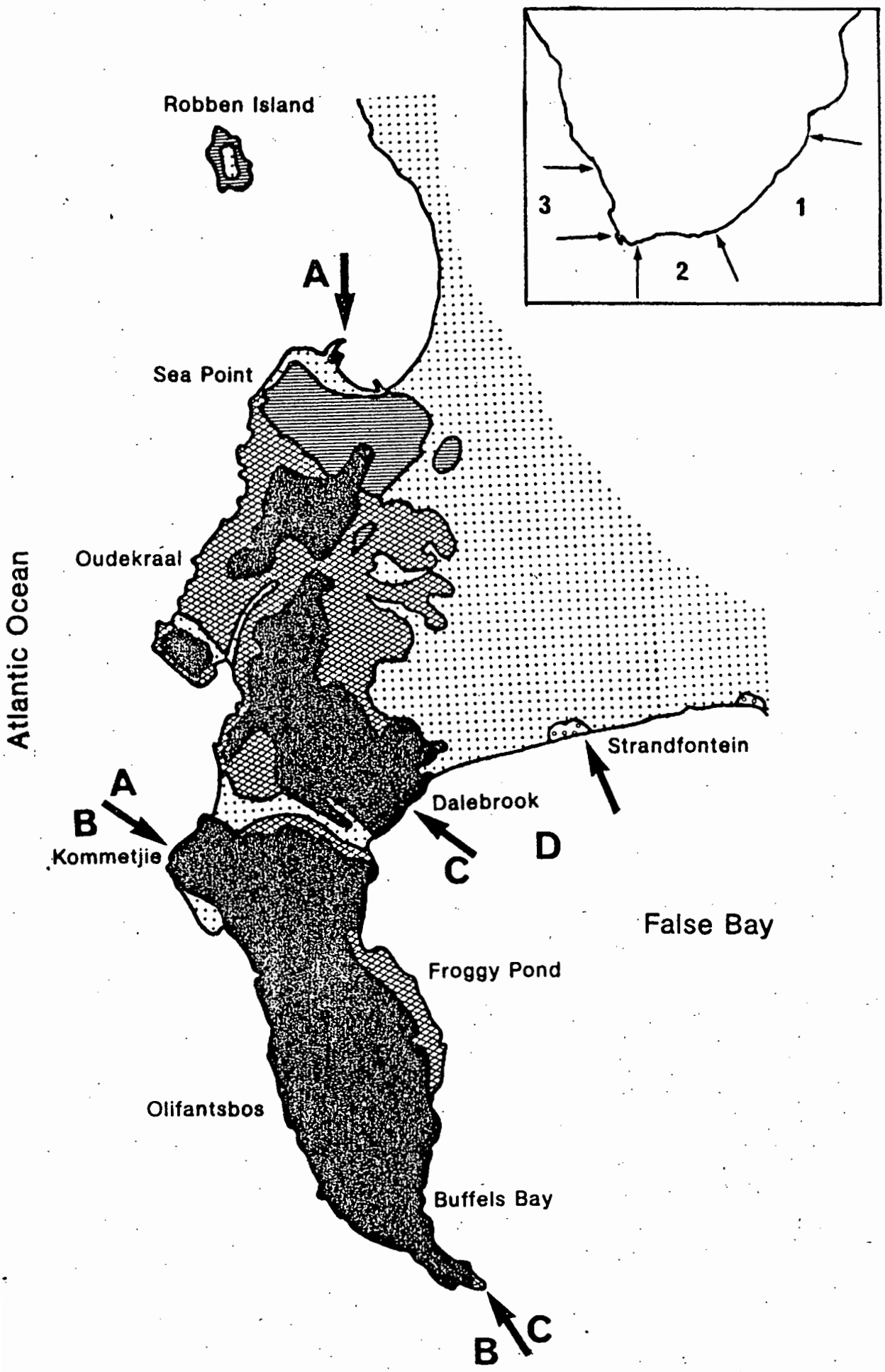
 = Malmesbury Shale

 = Table Mountain Sandstone

 = Cape Granite

 = Consolidated beach rock

 = Recent sand.


Robben Island
A
Sea Point
Oudekraal
Atlantic Ocean
A
B
Kommetjie
Dalebrook
C
D
Strandfontein
False Bay
Froggy Pond
Olifantsbos
Buffels Bay
B
C
3
1
2

STUDY AREA

Temperature

The coast of South Africa experiences almost pure semi-diurnal tides with a tidal range of approximately 2m. The intertidal biota has been divided by Stephenson (1944) into three main regions (see fig. 1.1). These follow a temperature gradient from the sub-tropical east coast through the south coast to the cool Atlantic west coast. The south coast biota (Port St. John's to Cape Agulhas) is composed of an east coast component spreading south from Natal, an endemic south coast component and elements of the west coast biota extending eastwards. The west coast biota (Port Nolloth to Kommetjie) is dominated by cold water species with a few south coast species which disappear farther north. A very few east coast species are also present. A number of ubiquitous forms are common to all three biota.

The Cape Peninsula and False Bay (from Kommetjie to Cape Agulhas) are considered by Stephenson (1944) to form a transitional area between the west and south coast biota. Although the exact position of the boundary between these two biotic provinces has been disputed the concept of an overlap region has been accepted by most authors (Brown and Jarman, 1978).

The situation is complicated because False Bay forms a pocket of very warm water out of sequence with the trend of temperatures along the coast. Populations characteristic of colder water exist both east and west of False Bay. Although in the northern part of the Peninsula temperatures are on the whole cooler on the west coast than on the east coast (Fricke and Thum, 1975) the difference is much less distinct towards the southern tip of the Peninsula.

Stephenson (1944) has divided the peninsular intertidal biota into four regions (fig. 1.1). These regions are based on temperature effects causing trends in the intertidal populations:

A Cape Town to Kommetjie - roughly typical west coast

B Kommetjie to Cape Point - west coast with increasing south coast component.

C Cape Point to Kalk Bay - modified south coast with important west coast influence.

D Kalk Bay to Muizenberg - similar to south coast east of Cape Agulhas with reduced west coast elements. This region extends beyond the Peninsula at least as far as Strandfontein.

For the purposes of this study only two temperature regimes were initially distinguished : cold (predominantly west coast biota) and warm (predominantly south coast biota).

Substrate

Geologically the Cape Peninsula consists of Table Mountain Sandstone (TMS) overlying Malmesbury Shale and Cape Granite (fig.1.1) Cape Granite is the only common igneous rock type present. All three of these rock types are exposed at various sites and all are fairly hard. Each rock produces a typical beach form due to characteristic weathering.

TMS is very stable chemically and weathers slowly. Grain size is small as the rock is composed of weathered quartz grains laid down by sedimentation and cemented by silica. It lies in almost horizontal beds and weathers into blocks generally forming broad, gently sloping beaches.

Malmesbury Shale has a very small grain size being originally formed from small silt and clay particles subsequently baked to hornfels by adjacent granite. It lies in steeply sloping or almost vertical beds and weathers as jagged, parallel ridges of rock running towards the sea and separated by gulley-like dips. These dips often form long, deep pools and allow an upshore extension of the lower zones. Shale usually forms gently sloping beaches. Exposures of shale occur only on the west coast of the Peninsula.

Cape Granite is coarse grained, usually with a rough surface. It occurs as huge rounded exhumed boulders, forming intertidal rock faces which are mainly steep or vertical and only rarely form intertidal pools.

In addition to these hard rocks outcrops of very soft consolidated beach rock occur along the northern coast of False Bay, notably at Strandfontein. Here the rock has a friable, crumbling nature and forms a long, low platform very much dissected by erosion and surrounded by long stretches of sandy beach on either side. Erosion effects produce a jagged surface with a complex network of small hollows and pools in the lower parts of the beach.

Wave exposure

The entire coastline of South Africa is very exposed. The west coast of the Peninsula and False Bay are subjected to continuous heavy swells due to north-west winds in winter and south-east winds in summer. The fetch for either wind is several thousand miles. Local topography and aspect result in conditions of greater or lesser exposure. For this study beaches were classified as either exposed or sheltered on the basis of long term observation and familiarity with the coastline. Aspect and topographic effects were taken into account in this classification along with subsequent observations of wave action during conditions of strong onshore swells. In European terms these categories would probably approximate to moderately and exposed/very exposed conditions.

METHODS

Preliminary examination of beaches revealed two important points:
(a) there is a wide diversity of beach types and each of the beaches examined was itself extremely heterogenous;
(b) use of line transects assumes the heterogeneity of a beach to follow a two-dimensional pattern, varying with vertical height and distance from the sea. In fact, however, horizontal position across the beach is also extremely important as the intertidal zones do not usually form regular bands of consistent breadth across the beach, but consist of a mosaic of roughly homogeneous zones. Because of this a straight line down the beach is likely to either miss some zones altogether or distort their apparent significance by passing through particularly wide or narrow parts of each zone. This error may be minimised using a series of parallel transects at each beach. However, this requires prohibitively more time, resulting in less detailed sampling and is subject, to a lesser degree, to the same criticisms as single transects.

To obtain a more accurate estimate of species biomass on the beach as a whole rather than along transect lines, each beach was mapped using aerial photographs in conjunction with field measurements. While this does not affect species biomass measurements for each zone it has important implications when the beach is considered as a whole as will be discussed in Chapter two.

Although the major zones (eg. cochlear, balanoid etc.) were obvious it was found that these were often extremely heterogeneous. Consideration of these as homogeneous zones would lead to often gross misrepresentation of species abundance on the beach as a whole, again an important point in the section on similarity analysis (Chap. 4). Separate "zones" were therefore recognised as approximately homogeneous sub-communities identified by the dominance of different species.

Although this method entails a more intensive sampling of each beach it is felt to yield much more accurate results when used in conjunction with mapping techniques. The heterogeneity of beaches and the significance of variation across the beach may be seen in figs. 1.5 - 1.15.

TABLE 1.1 CLASSIFICATION OF BEACHES

NAME	ABBRE-VIATION	TEMPE-RATURE	EXPOSURE	SUBSTRATE
Sea Point	SPT	C	E	Malmesbury Shale
Oudekraal A	OKA	C	S	Granite
Oudekraal B	OKB	C	E	Granite
Robben Island	ROB	C	E	Malmesbury Shale
Olifantsbos	OFB	C	S	Table Mountain sandstone
Kommetjie	KOM	C	S	TMS
Buffels Bay A	BFA	W	S	TMS
Buffels Bay B	BFB	W	S	TMS
Froggy Pond A	FPA	W	S	Granite
Froggy Pond B	FPB	W	E	Granite
Dalebrook	DBK	W	E	TMS
Strandfontein	STR	W	E	Beach rock

Beach selection

A range of combinations of different conditions of wave exposure, substrate and temperature exists around the Cape Peninsula. Unfortunately some of the possible combinations are not found in the Peninsula. For example Malmesbury Shale outcrops occur only on the west coast and consolidated beach rock occurs only along the north coast of False Bay.

Twelve beaches were therefore selected to cover as wide a spectrum as possible of these combinations, including six west coast beaches and six False Bay beaches (see Table 1.1 for a summary of conditions on the beaches selected).

Sampling

At each beach a transect was laid down from approximately HWS to LWS during conditions of spring tides. A transect profile was derived following the techniques of Day (1969) and the major zones and subzones identified. Topographic conditions often resulted in some zones lying off the transect line so during sampling this line was not strictly adhered to. The vertical height of such zones was then measured independently. Transects thus represent not so much a straight line as a "composite" profile including all zones. Identified zones were sampled quantitatively by scraping 1 m^2 or 0,25 m^2 quadrats supplemented by belt transects within each zone where larger species with markedly clumped distribution occurred. Where necessary duplicate quadrat samples were taken but for many zones single large samples were used. This was partially because the tremendous heterogeneity of beaches necessitated large numbers of samples and partially because zones were recognised on the basis of being very distinct subcommunities.

Samples were processed immediately when possible or else preserved in 5 % formalin and subsequently sorted to species level. Dry weights were obtained by oven drying at 60°C for at least 24 hours and weighing to ,0001 g. Heavily calcified species were treated with 1 molar HNO_3 to remove inorganic material before drying

and in the case of limpets the shell was removed before drying and weighing.

Length/weight curves based on power curve equations were drawn up for the larger, more common species (Table 1.2) so that only length measurements were subsequently required. This proved to be particularly time saving in the case of common calcified species. The mussel Kellya rubra and the winkle Eatoniella niger are both very small ($<$ 1mm) and often very numerous. For each of these species a mean acidised dry weight was derived for three samples of 100 individuals. (Table 1.2) These species were subsequently counted and dry weight derived by extrapolation.

Studies on energy flow hinge on biomass values and these were used in subsequent analyses. Data on numbers of individuals give no indication of the levels of biomass involved and are often impossible to obtain for algae so that comparative analyses including algae are not feasible.

TABLE 1.2 : BODY SIZE/ACIDISED DRY MASS REGRESSION EQUATIONS FOR SOME COMMON INTERTIDAL SPECIES.

(y = acidised dry mass; x = maximum length or, for species marked with *, maximum diameter).

SPECIES	REGRESSION EQUATION	COEFFICIENT OF DETERMINATION (r^2)
Pelecypoda		
Aulacomya ater	$y=0,00049503x^{1,9832}$	0,96
Choromytilus meridionalis	$y=0,00732176x^{0,8241}$	0,86
Perna perna	$y=0,00260219x^{1,3402}$	0,86
Gastropoda		
Burnupena spp.	$y=0,00000714x^{3,1940}$	0,90
Fissurela mutabilis	$y=0,00009937x^{2,2694}$	0,80
*Oxystele sinensis	$y=0,00114377x^{1,7681}$	0,77
*Oxystele variegata	$y=0,00001445x^{3,5980}$	0,98
Patella barbara	$y=0,00000689x^{3,2537}$	0,90
Patella cochlear	$y=0,00001987x^{2,6699}$	0,88
Patella granatina	$y=0,00831103x^{1,2483}$	0,67
Patella granularis	$y=0,00012590x^{2,2035}$	0,92
Patella longicosta	$y=0,00012851x^{2,0898}$	0,87
Patella oculus	$y=0,00038411x^{2,0868}$	0,98
Siphonaria aspera	$y=0,00005673x^{2,6378}$	0,69
Siphonaria capensis	$y=0,00044894x^{1,74}$	0,74
Siphonaria deflexa	$y=0,00010551x^{2,2344}$	0,89
Echinoidea		
Thais dubia	$y=0,00194531x^{1,7181}$	0,92
*Parechinus angulosus	$y=0,00041724x^{2,2479}$	0,95

mean acidised dry mass for 3 samples of 100 individuals :

Eatoniella nigra	0,0081g
Kellya rubra	0,01246g

CHAPTER 2 : ZONATION

INTRODUCTION

Isaac (1937) has given a detailed description of algal zonation for the north/central and southern regions of the west coast of the Peninsula. Detailed descriptions have also been given of the intertidal zone at Oudekraal (west coast) and St. James (False Bay) by Bright (1938) and Eyre (1939) respectively. Subsequently Stephenson (1939) produced a general model for biotic zonation in the South African coast as a whole which is still in use. Despite this work and the generalised description of the Peninsula given by Stephenson (1944) a quantitative survey of different beach types in the Peninsula is still lacking.

In this chapter a generalised account of zonation and the occurrence of the major species is given. This is derived from the description of zonation and species abundance at the twelve beaches examined.

GENERALISED INTERTIDAL ZONATION IN THE CAPE PENINSULA

The following basic pattern of zonation was found to apply. It accords with the models produced by Isaac (1937) and Stephenson (1939, 1944) and each beach conforms to a greater or lesser extent.

1. Subtidal algal fringe

This is generally an algal fringe which is wholly subtidal although occasionally it combines with the lower cochlear zone to form a separate cochlear/weed zone. Usually a single algal species dominates but at some beaches several species share dominance. Common dominant species are Bifurcaria brassicaeformis (both coasts), Champia lumbricalis (particularly the west coast), Plocamium spp. and Hypnea spicifera (especially False Bay). This zone often yields a very high biomass of algae and contains an extremely rich complex of associated fauna of small crustaceans, errant polychaetes and small molluscs among the fronds and holdfasts. Whenever large quantities of algae

are mentioned in any of the lower intertidal zones the presence of this fauna is implied. Amphipods and Isopods are particularly important, especially Hyale spp., Lysianassa spp., Paridotea spp., Caprellina longicolis and Paramoera capensis among the amphipods and Dynamenella spp. (particularly D.huttoni and D.australis), Exosphaeroma spp. (notably E. laeviusculum and E.varicolor) and Cymodocella sublevis and C. pustulata among the isopods. Among the polychaets Syllis spp., Platynereis dumerillii and Pseudonereis variegata are abundant. Small molluscs present generally include Gibbula spp., and Tricolia spp. Small nematodes may also be common.

On exposed beaches dense communities of filter-feeders generally occur in this zone. These communities are dominated by the mussel Aulacomya ater in conjunction with the barnacle Octomeris angulosa on the west coast and the tunicate Pyura stolonifera and the mussel Perna perna in False Bay.

2. Cochlear Zone

This zone is usually clearly defined, being completely dominated by Patella cochlear and small algae. These include encrusting and coraline forms such as Jania sp., Lithophyllum spp. and especially Arthrocardia sp. as well as Splachnidium rugosum, Cladophora capensis, Gelidium pristoides and Gigartina stiriata. Symbiotic amphipods associated with P. cochlear also occur (Branch, 1975a). In some cases varying densities of P. cochlear and the local abundance of other species (such as Aeodes orbitosa) warranted the recognition of separate lower, middle or upper cochlear zones. Strandfontein is the only beach lacking P. cochlear (see below) and P. barbara occupies the equivalent zone here.

3. Balanoid zone

This is the middle region of the shore extending from the cochlear zone to the Littorina zone at the top of the shore.

The balanoid zone is usually clearly divisible into lower, middle and upper components although some species (eg. Oxystele

variegata, Kellya rubra, Eatoniella niger and Patella granularis) are often common over the entire balanoid. Great diversity appears in this zone and different complexes of species were recognized as separate zones where necessary.

(a) Lower balanoid

A large variety of algae is generally present including Hypnea spicifera, Plocamium spp., Gelidium spp., Pterosiphonia cloiophylla, Gigartina spp., Aeodes orbitosa and Arthrocardia spp. Certain animal groups are also important here, notably limpets (eg. Fissurella mutabilis, Patella granatina, P. granularis, P. oculus, P. barbara and P. longicostis) and often whelks (eg. Burnupena spp. and Thais spp., particularly B. delalandii and T. dubia). Large colonies of sedentary polychaets such as Gunnarea capensis and Pomatoleios kraussi sometimes occur. Barnacles are generally very sparse but Balanus algicola and Octomeris angulosa may be present.

(b) Middle balanoid

Fewer species of algae are present here, but Gelidium pristoides, Ulva sp. and Gigartina spp. are often abundant. Mussels and whelks are also fewer while barnacles (mainly Octomeris angulosa and Tetraclita serrata) become important especially on exposed beaches. Patella granularis and Oxystele variegata become more abundant here and the limpets Siphonaria spp. and Helcion pectunculus are sometimes present.

(c) Upper balanoid

The few algae present (usually only Porphyra capensis) are generally not abundant. Barnacles especially Tetraclita serrata but now including Chthalamus dentatus tend to be abundant as do Siphonaria spp. and often H. pectunculus. On some beaches separate zones in the upper balanoid occur. Siphonaria may dominate large areas, especially if many shallow pools are present, forming a separate Siphonaria zone. Dense clumps of the alga Porphyra capensis may also be present, sheltering numerous amphipods, usually Hyale grandicornis or H. diastema.

Overlap of this Porphyra zone with the Siphonaria or Littorina zones sometimes occurs.

4. Littorina zone

This represents the littoral fringe and is generally exclusively occupied by the winkle Littorina africana knysnaensis, which often attains great density. Scattered specimens of Thais dubia may also be present.

5. Pools

Although isolated pools do not occur on granite beaches, due to their topography, they are more or less common throughout the balanoid zone on other beaches, and were divided into lower, middle and upper balanoid pools. Pool species richness declines in the upper regions but generally remains higher than the richness of surrounding zones. Pools can be very rich in species but are often dominated by algae(eg. Ulva spp., Gymnogongrus dilatatus, Aeodes orbitosa, Cladophora spp., and Gigartina spp.). The urchin Parechinus angulosus, anemones such as Pseudactinia flagellifera and Bunodosoma capensis and small chitons (eg. Acanthochiton garnoti and Chiton nigrovirescens) are frequently abundant. Other forms generally present include asteroids (eg. Henricia ornata and especially Patiriella exigua), limpets (eg. Helcion pruinosus and Crepidula porcellana), ophiuroids (especially Amphipholus squamata and Amphipolus integer) and small winkles (Tricolia spp.)

The amphipod and isopod fauna of pools is often rich and other common balanoid species are often very numerous in pools (eg. Oxystele variegata, Burnupena spp., Siphonaria spp. and sometimes various mussels).

SPECIES RICHNESS

Species richness declines in these zones in an upshore direction on all beaches (figs. 1.2-1.4). This is probably due to high niche heterogeneity in the lower shore coupled with more

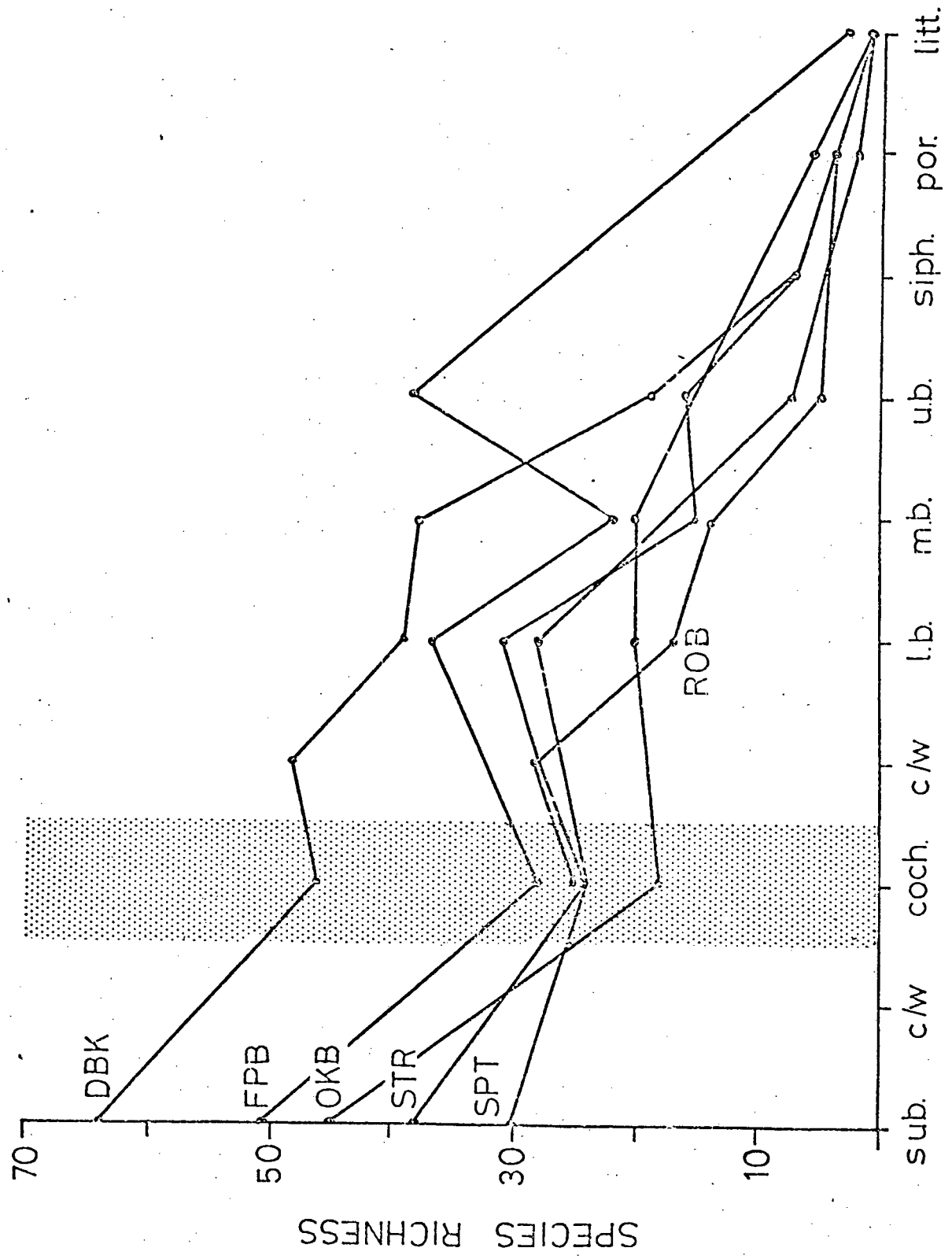


Fig. 1.2 The relationship between zonation and species richness on exposed beaches.

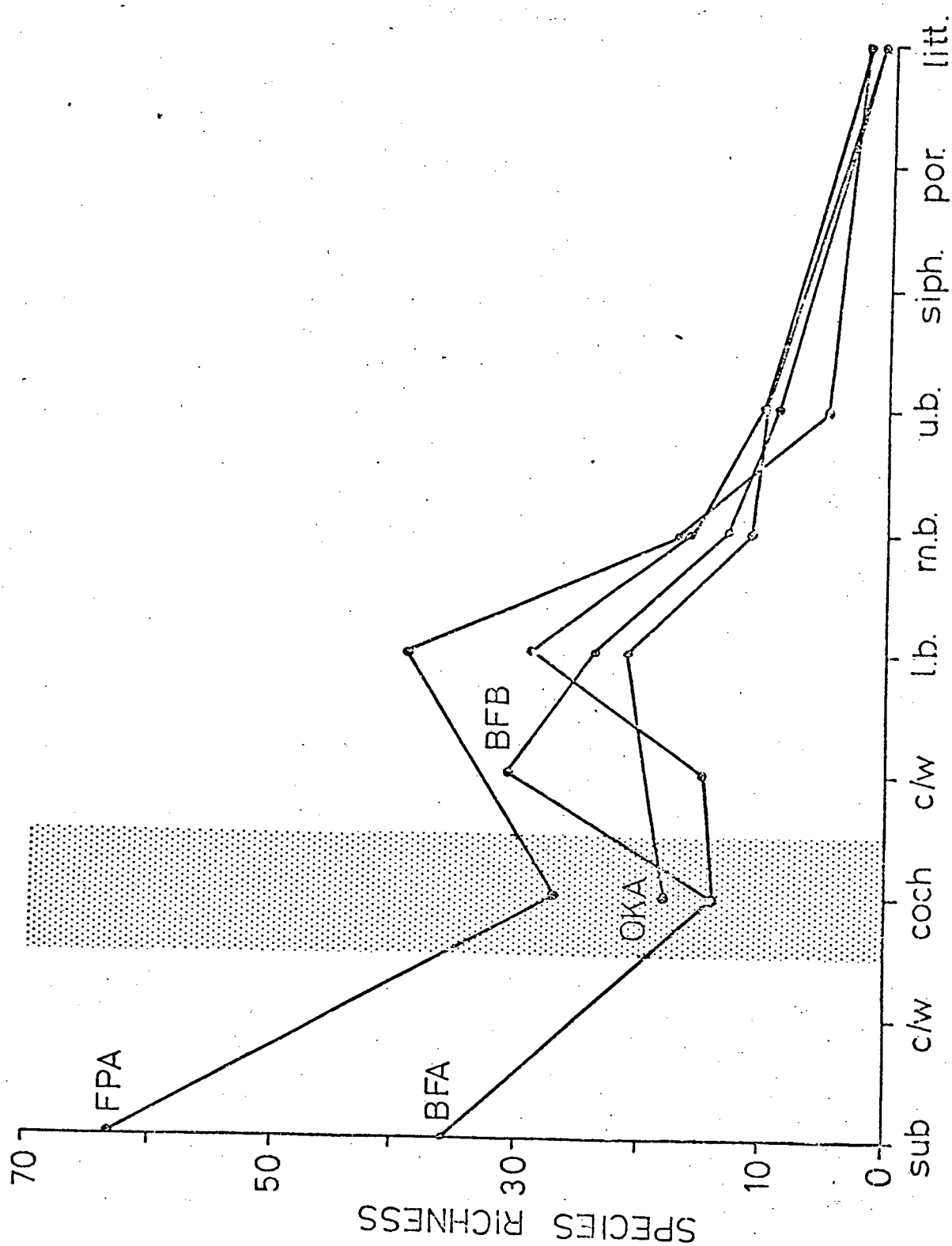


Fig. 1.3 The relationship between zonation and species richness on sheltered beaches.

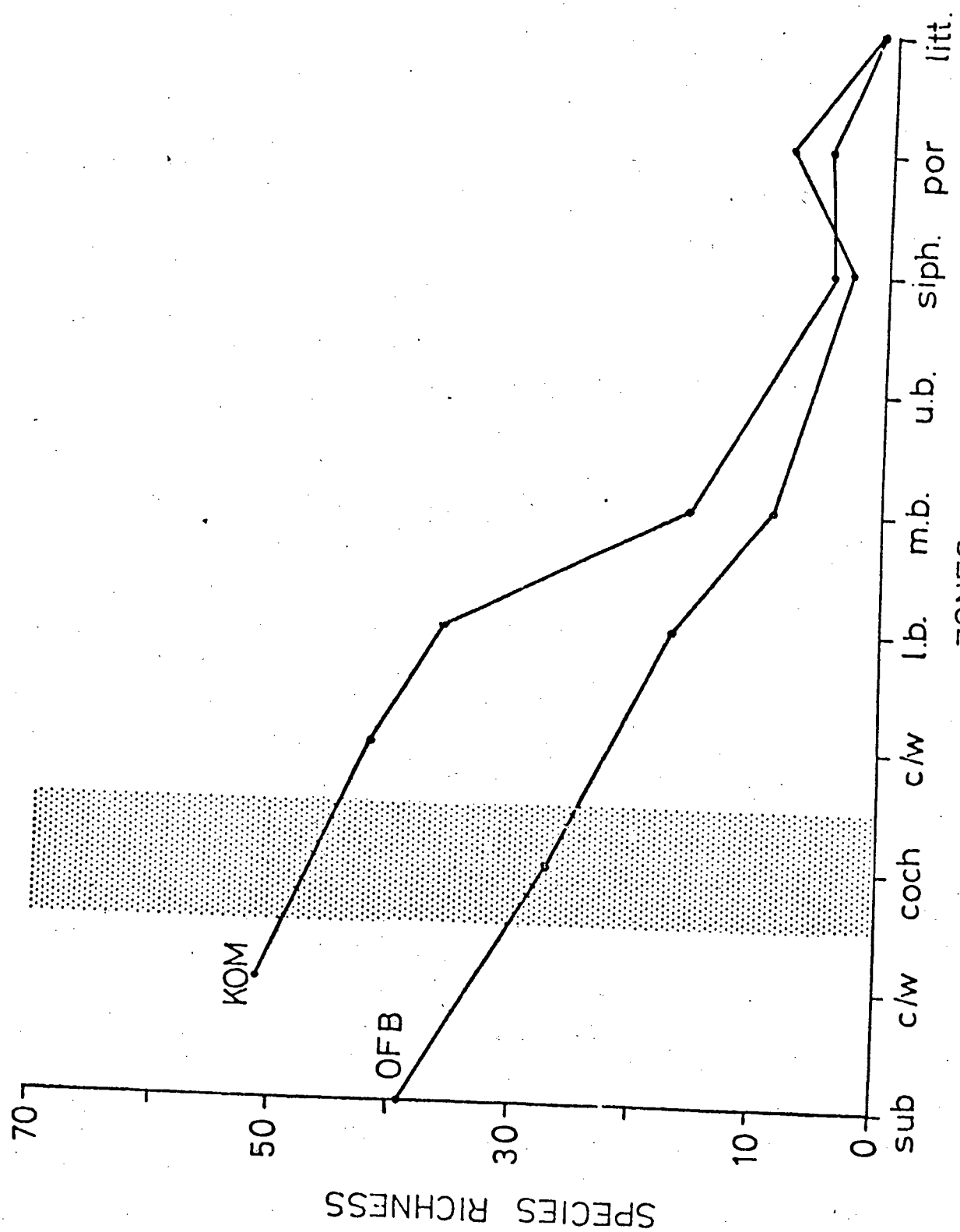


Fig. 1.4 The relationship between zonation and species richness on aberrant sheltered beaches.

extreme and less stable conditions at the top of the littoral zone (Newell, 1979).

An important additional point is that on all except two beaches (Kommetjie and Olifantsbos) richness is lower in the cochlear zone than in adjacent zones. This is due to domination of this zone by Patella cochlear. P. cochlear is absent from Strandfontein but is replaced by P. barbara and the same effect occurs in the equivalent zone here (fig. 1.2). Algal biomass is generally very low in the cochlear zone due to grazing (see p.73) and this probably results in a decrease in niche availability. At both Kommetjie and Olifantsbos zonal patterns of algal biomass are unusual (p. 77 and figs. 1.30 - 1.32) and there is a direct correlation with patterns of species richness. The importance of niche availability is further indicated by the high species richness of the upper balanoid at Froggy Pond B (fig. 1.2). This zone is dominated by a very dense bed of Octomeris angulosa which offers a wide range of microhabitats to smaller forms.

DESCRIPTION OF THE BEACHES EXAMINED

In the following section the more important physical and biotic features of each beach are briefly described. Maps are provided and beach profiles are included in the section on trophic zonation (p.59). Fig. 1.16 shows a generalised profile form for the three major substrate types.

A total of 310 species were identified and are listed, along with the trophic compartment to which each species was allocated in Table 1.3 (Appendix 1). The number of sub-communities on each beach varied considerably depending on heterogeneity and a total of 113 were recognised between all 12 beaches. The resultant data matrix of species vs. sub-communities is thus very large. Although analyses were performed on the full matrix the data are therefore compressed for presentation. Species biomass values are given as mean biomass $.m^{-2}$ for all zones occupied on each beach in Table 1.4 (Appendix 2). The species are coded according to the list number given in Table 1.3. A full data matrix of species biomass in each zone on each beach is housed in the Zoology Department of the University of Cape Town.

1. WEST COAST

Robben Island (ROB) (see fig. 1.18).

An exposed beach of Malmesbury Shale. The long alternate ridges and gulleys, formed by the characteristic weathering of this rock, run perpendicular to the shore line. The beach is steep in the Littorinazone then slopes gently across the balanoid zone to the cochlear zone which is also steep. The subtidal fringe of algae merges with the cochlear zone forming two separate cochlear/weed sub-zones above the cochlear. The lower of these (mid-cochlear) is a zone of extremely dense Bifurcaria brassicaeformis (the dominant subtidal species at Seapoint). This is backed by an upper cochlear zone with large quantities of Champia lumbricalis (the fringing species at Oudekraal B). The lower balanoid is dominated by the barnacle Tetraclita serrata.

Aerial photography and mapping of this beach were not possible due to the presence of a high security prison on the island.

Seapoint (SPT, fig. 1.5)

This is a gently sloping exposed beach of Malmesbury Shale. It is structurally similar to Robben Island with alternate ridges and gulleys which cause zones to be extended up or down the shore resulting in a complex mosaic of zones. Dense beds of Bifurcaria brassicaeformis form a subtidal fringe to the relatively narrow cochlear zone. No distinct mid-balanoid is present, this being replaced by an extended lower balanoid. A large number of elongated, deep pools are present, particularly in the lower balanoid, containing a large variety of species. Scattered patches of Porphyra capensis occur in the Littoria zone.

FIGS. 1.5 - 1.15 Maps of 11 beaches examined showing intertidal zonation.

● = subtidal fringe

○ = cochlear zone

▲ = Lower balanoid

△ = Mid-balanoid

■ = Upper balanoid

▫ = Siphonaria zone

 = Porphyra zone

L = Littorina zone

 = pools

Subdivisions of the major zones are denoted 1,2 etc.

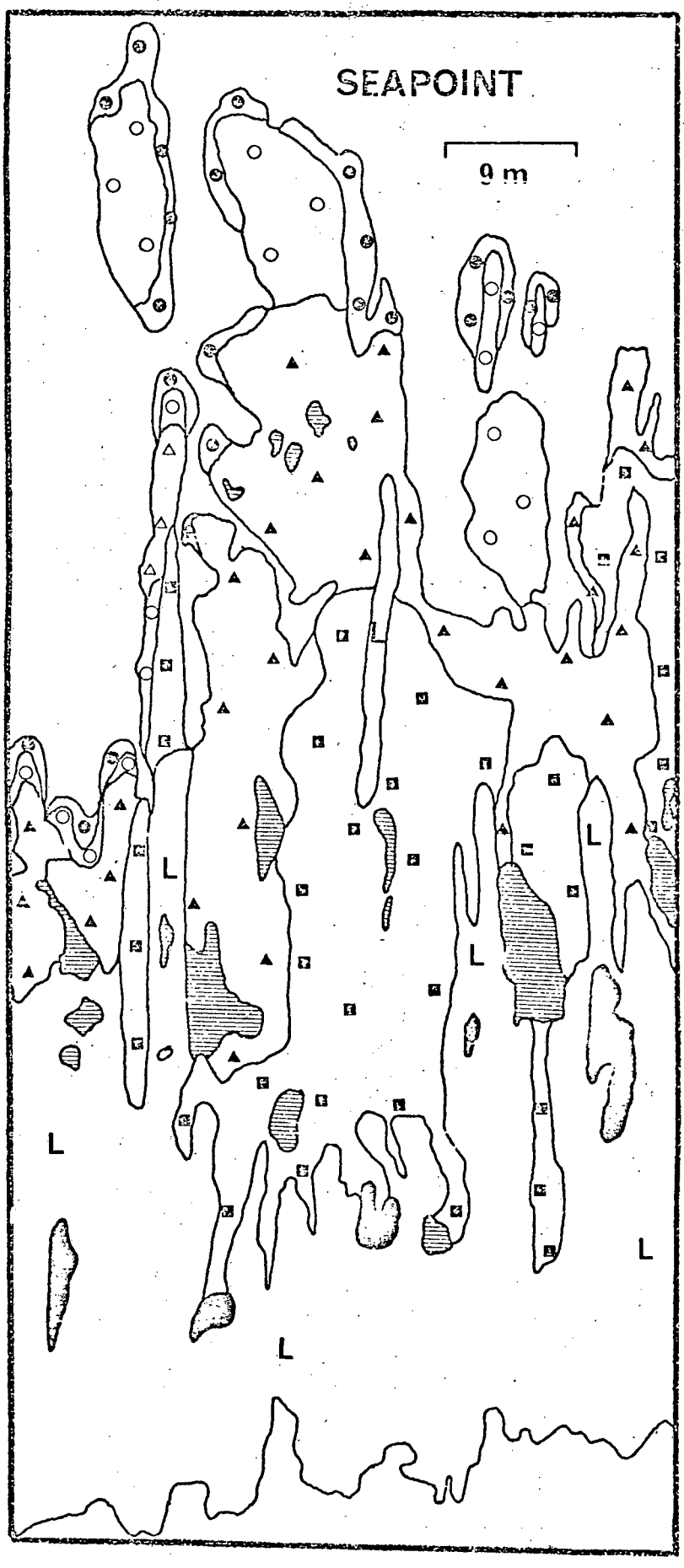


Fig. 1.5

Oudekraal

Two beaches were examined at Oudekraal as they provide a good example of an exposed and sheltered beach closely adjacent and composed of the same substrate (Cape Granite).

Oudekraal A (OKA, fig. 1.6)

This is a sheltered beach lying in a small bay. It slopes quite steeply below the Littorina zone so that the lower zones are narrow. The beach is composed of small granite boulders approximately 0,3 - 0,5 mm in diameter, the larger rocks forming isolated units of mid balanoid within the low balanoid (see map). The instability of the substrate results in a lower species richness, particularly of sedentary species and limpets, only 4 limpet species occurring here. The absence of an algal infratidal fringe, the low algal richness and the consequent poverty of epifauna may also be attributed to this. Water drains away between the boulders so that no pools are found here.

Several species are common beneath the rocks however and oligochaets are especially abundant beneath the kelp debris towards the top of the beach.

Oudekraal B (OKB, fig. 1.7)

An exposed position near the end of a small promontory. The beach is composed of huge granite boulders of up to 10 m diameter. The dense Champia lumbricalis beds forming the subtidal fringe are rich in species housing a particularly large variety of polychaets. The mid-balanoid is backed by a long gulley running parallel to the shore and subjected to powerful surge effects. Filter-feeders are abundant, particularly in the mid-balanoid and gulley.

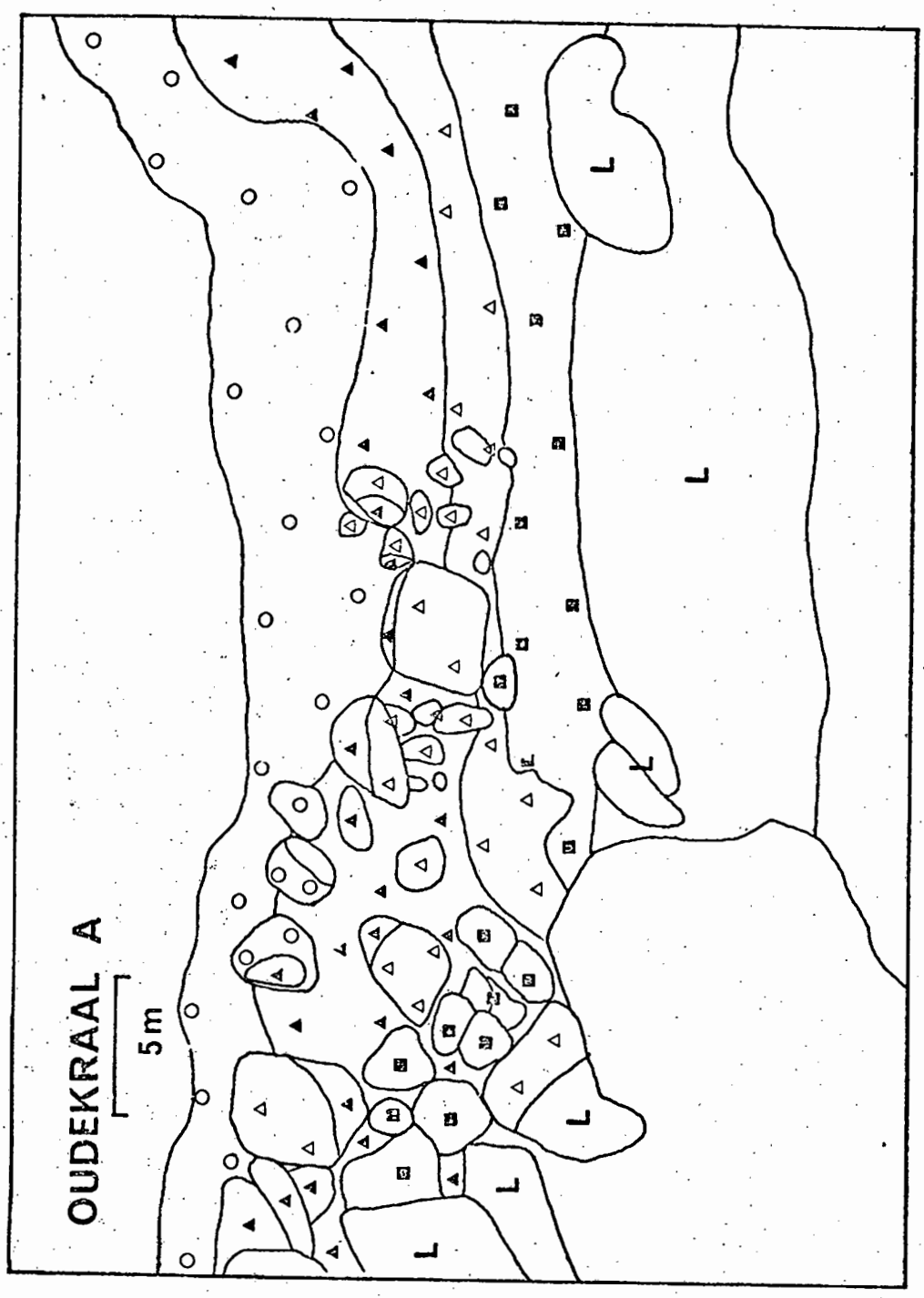


Fig. 1.6

Kommetjie (KOM, fig. 1.8)

The beach examined here lies almost perpendicular to the predominantly north-west onshore swells and is consequently sheltered. It is composed of a flat platform of Table Mountain Sandstone broken up by a number of large squarish rocks (around 6 feet high) in the Littoria zone. The cochlear zone is ill-defined and merges with the subtidal fringe to form a cochlear-weed zone. Above this is a separate and scattered upper cochlear/weed zone containing much Aeodes orbitosa. A narrow but distinct zone occurs at the upper-middle balanoid junction. The upper balanoid is formed by an extensive Siphonaria zone where this genus is extremely abundant. A separate Porphyra zone also occurs. Shallow pools are common in both the lower balanoid and Siphonaria zones.

Olifantsbos (OFB, fig. 1.9)

A sheltered beach at the southern end of Olifantsbos bay, formed by a long, gently sloping tongue of Table Mountain Sandstone forming a small peninsula. It is surrounded, particularly to the south by a dense bed of Champia lumbricalis. A large number of pools occur in the balanoid as the beach is fairly flat on top, though slightly steeper around the margins. The upper balanoid is particularly diverse and was divided into a number of distinct zones. Siphonaria is abundant in these zones.

2. FALSE BAY

Buffels Bay

Two beaches were examined here as they provide a comparison of a beach of small boulders (BFB) and one composed of huge blocks of rock (BFA). Both beaches are composed of Table Mountain Sandstone.

Buffels Bay (BFA, fig. 1.10)

Both Buffels Bay beaches lie in a medium-sized bay and are relatively sheltered. BFA is composed of a series of large rectangular blocks of TMS of up to about 6 - 8 m in length. A very dense

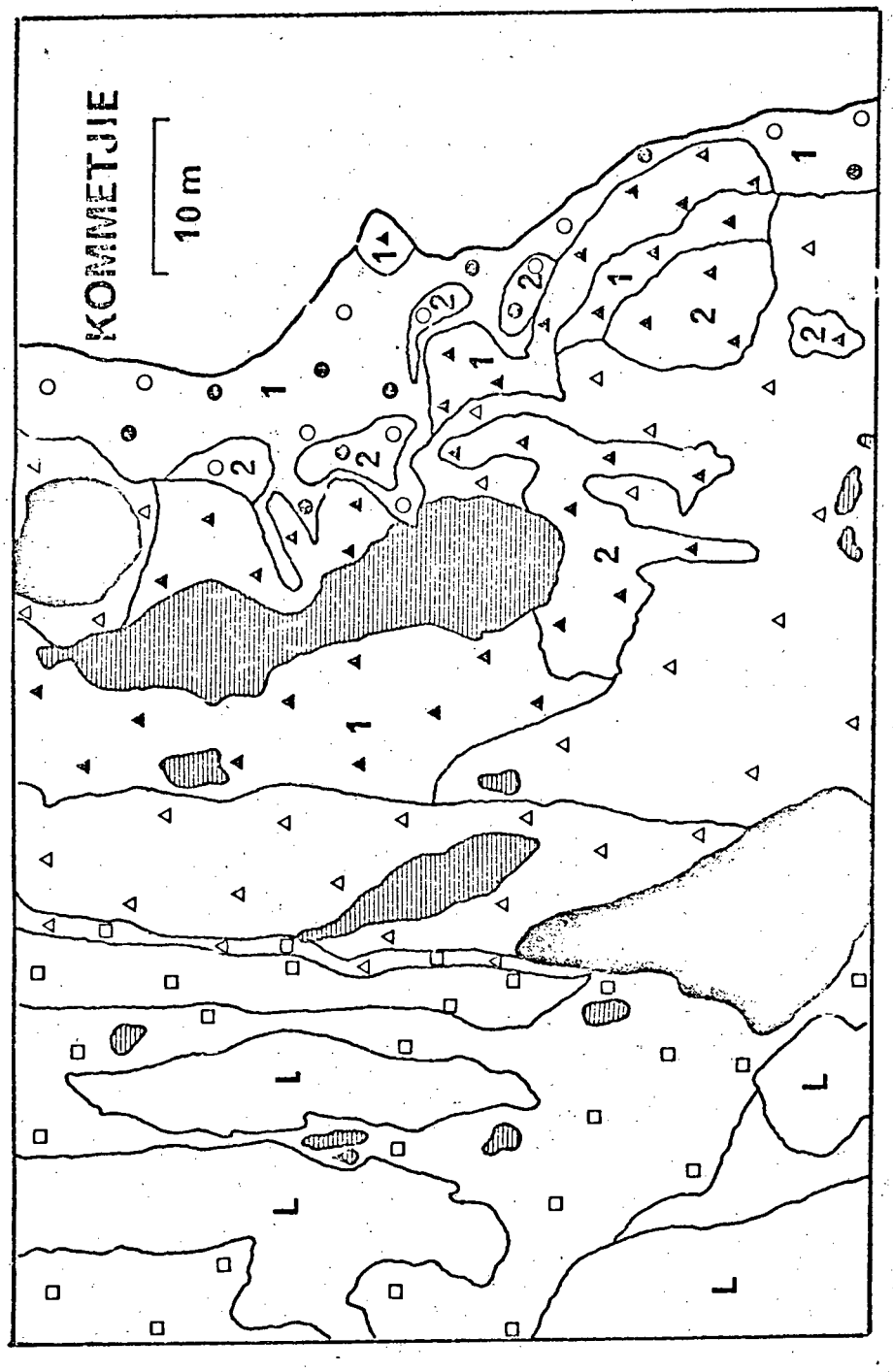


Fig. 1.8

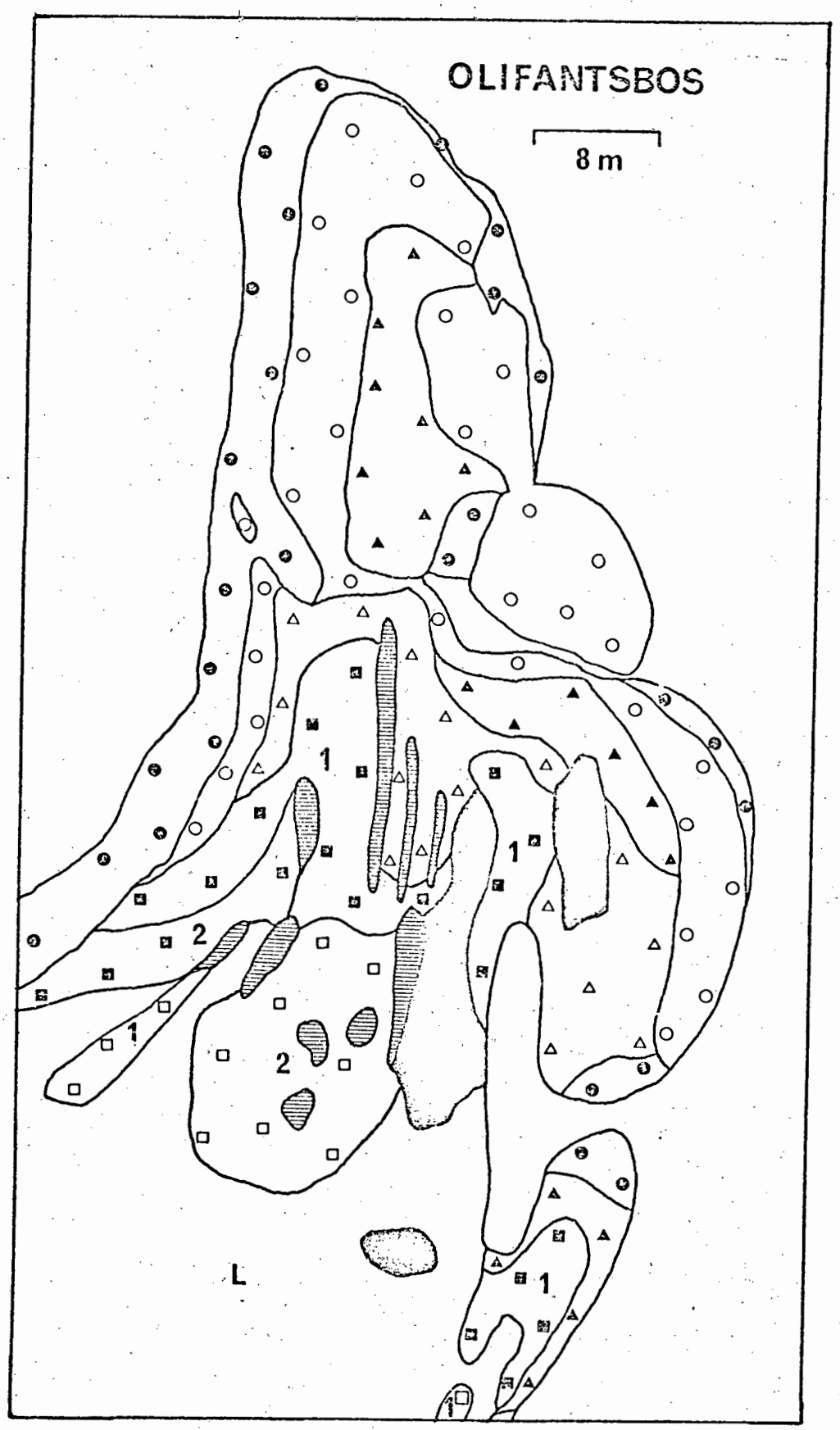


Fig. 1.9

bed of Bifurcaria brassicaeformis fringes the beach and parts of the lower balanoid are dominated by Bifurcariopsis capensis, forming a separate zone. The mid balanoid is diverse and is divided into a number of distinct, homogenous sub-zones. These are dominated by Siphonoria spp.; Patella granularis/Tetraclita serrata and Helcion pectunculus/Oxystele variegata/Patella oculus respectively. The uppermost of these zones is littered with small boulders which are almost devoid of algae and sedentary forms. H. Pectunculus and O. variegata are abundant here. Parts of the Littorina zone are isolated by sand.

Buffels Bay B (BFB, fig. 1.11)

This beach is more gently sloping and sheltered than BFA. It is composed of small relatively unstable boulders (about 0,3-0,5 m in diameter) and in consequence species richness is low. As with the other boulder beach, OKA, sedentary forms are not abundant and no fringing weed bed occurs though in this case a large offshore kelp bed of Ecklonia maxima extends nearly to the cochlear zone. (Two extensive, but shallow and particularly barren pools are found in the lower balanoid. The rocks forming the bottom of these are much smaller, about 10 cm in diameter and only Parechinus angulosus is common.) The presence of occasional large boulders results in odd outcrops of the Littorina and mid-balanoid zones low down on the shore (see map).

Froggy Pond

The occurrence of two beaches on opposite sides of a granite outcrop at this site allows a comparison of an exposed and a sheltered warm coast, granite beach. The boulders on both beaches are particularly large, being up to about 15-20 m across.

Froggy Pond A (FPA, fig. 1.12)

This beach is on the leeward side of the set of boulders and is sheltered. It is flattish in the lower regions becoming steeper in the upper zones along the face of a large boulder. A wide and very dense bed of Bifucaria brassicaeformis (containing an exceptionally wide diversity of

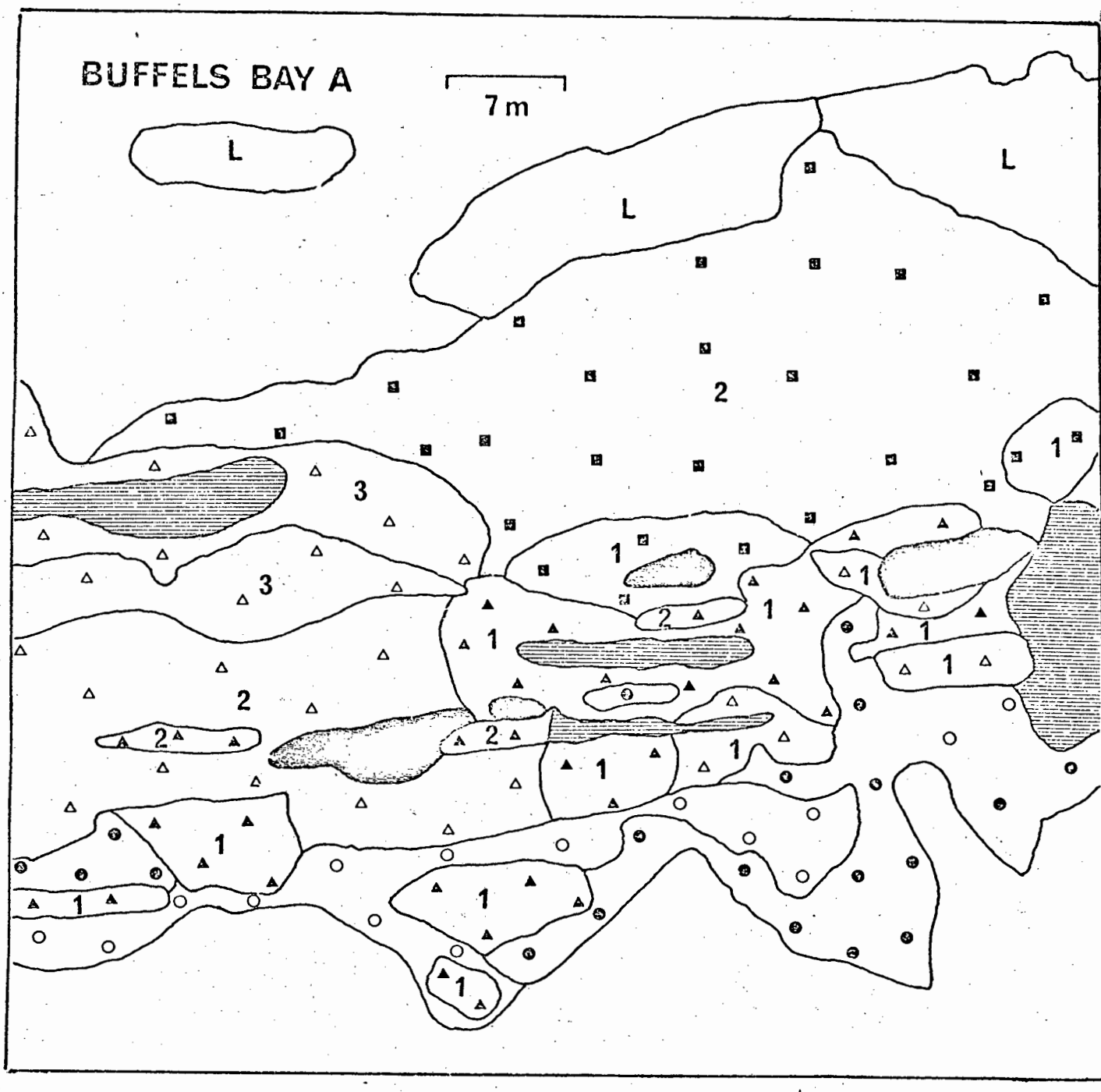


Fig. 1.10

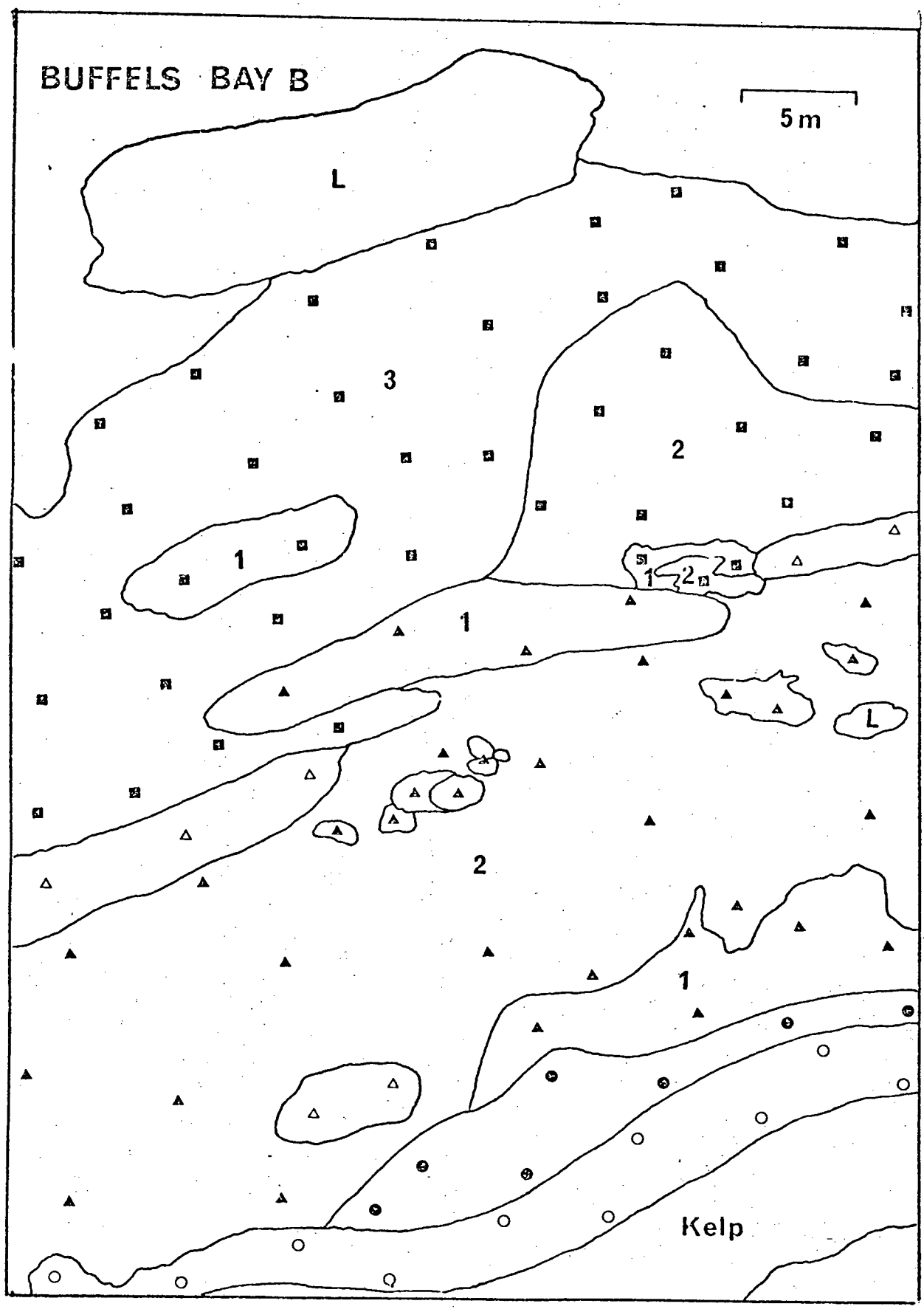


Fig. 1.11

worms, small molluscs and crustaceans) blends into the lower cochlear forming a separate cochlear/weed zone. The zones rise in a clear sequence from the cochlear zone to the steeper and narrower balanoid zones. Few filter-feeders are present except for a narrow band of Tetraclita serrata in the upper balanoid. Two long deep gulleys run up from the cochlear to the Littorina zone containing a separate and distinct biota.

Froggy Pond B (FPB, fig. 1.13)

This lies on the seaward side of the same set of boulders and is exposed to considerable surge effects due to the SE swells. It is rather steeper than FPA but similarly levels off slightly at the bottom of the shore. A fringe of algae is present, composed of a number of species (notably Ploconium cornutum and Pterosiphonia cloiophylla) in contrast to FPA. P. cochlear is low in abundance and the cochlear zone is small, much of the lower region being occupied by various filter-feeders including mussels and Pyura stolonifera. Two distinct low balanoid zones occur.

No distinct mid balanoid occurs and the upper balanoid is very clearly divided into an upper zone where Octomeris angulosa is very dense and a lower zone of lower density. The individual barnacles tend to be much smaller in the upper of these two zones.

The whole beach is dominated by filter-feeders and O. angulosa extends, in reduced numbers, down into part of the lower balanoid.

Dalebrook (DBK, fig. 1.14)

A long, flat, gently sloping beach of Table Mountain Sandstone, exposed particularly to south-east swells. The cochlear zone drops sharply to an extremely wide and gently sloping subtidal fringe. The algae of this fringe are much less dense than in most cases and include a variety of species. These support a wide range of polychaets, crustaceans and small molluscs. A long gulley containing numerous Parechinus angulosus and many other species extends from the cochlear zone up to the Siphonaria zone.

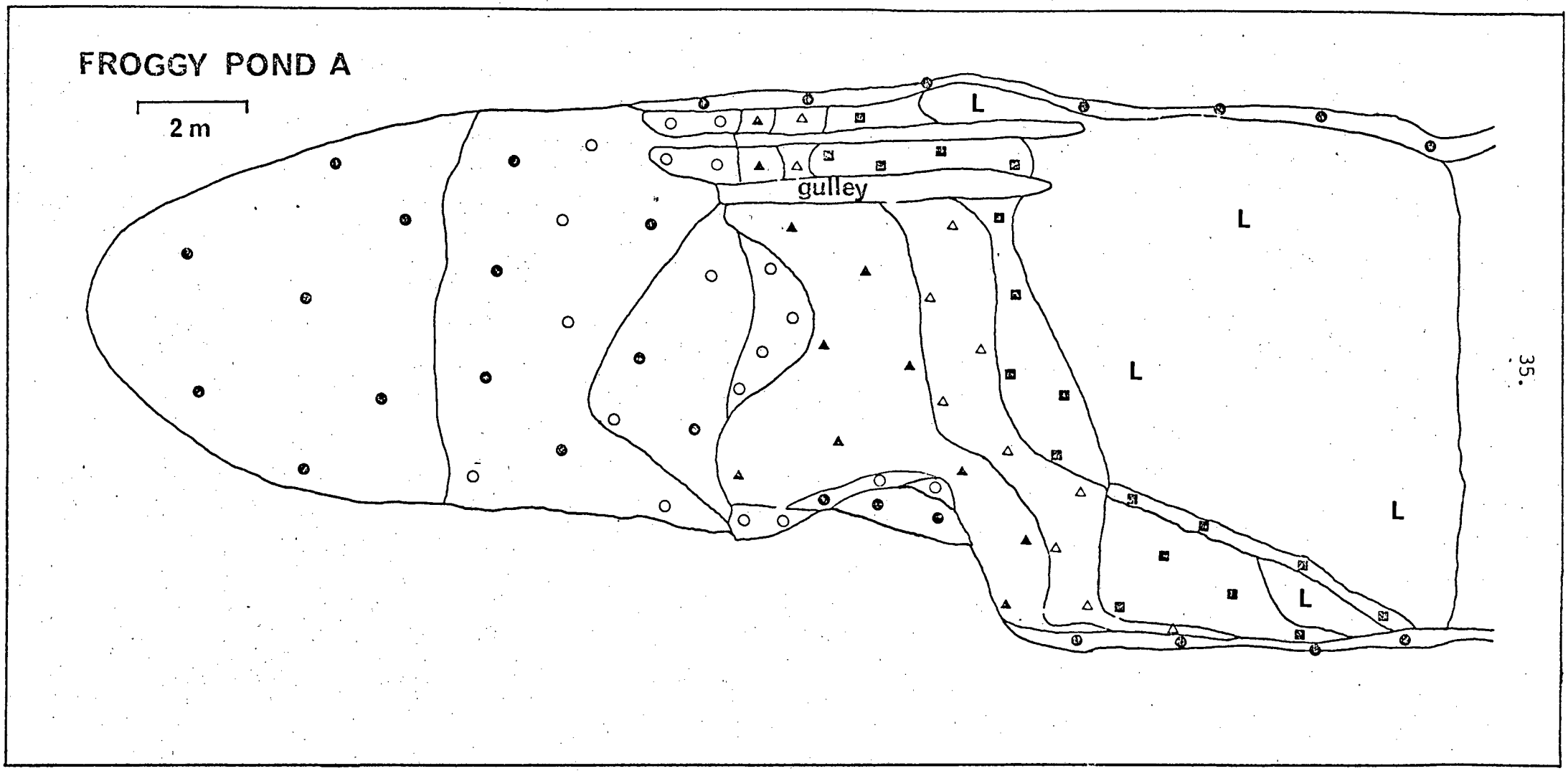


Fig. 1.12

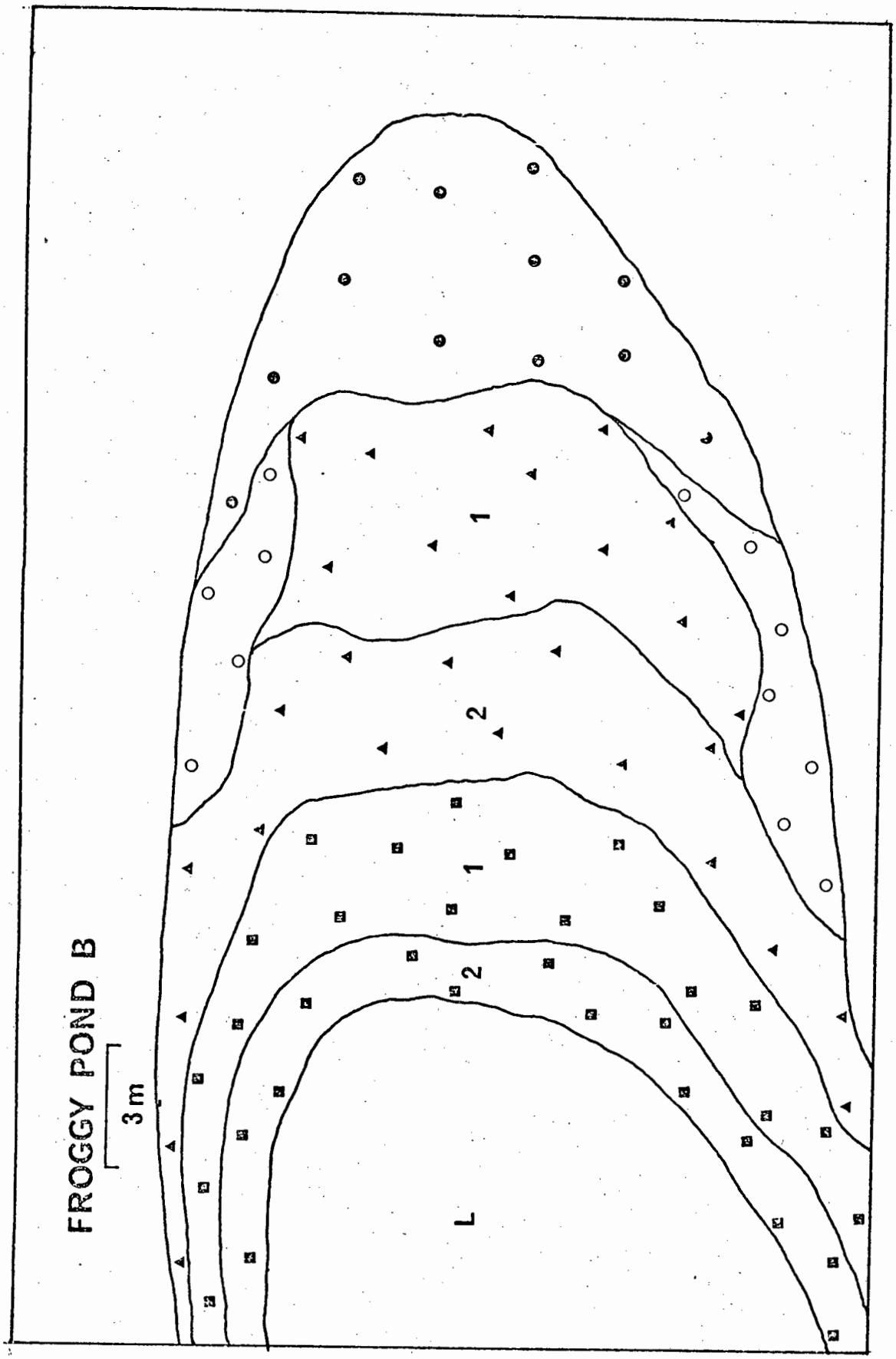


Fig. 1.13

The lower balanoid is dominated chiefly by Gigartina radula and the mid balanoid by Ulva sp., Gelidium pristoides and dense colonies of Tetraclita serrata. There is a distinct, wide Siphonoria zone within which a set of rocks support a separate upper balanoid biota. The Littorina zone is backed by another set of rocks at about the MHWS mark.

Strandfontein (STR, fig. 1.15)

This is an exposed beach. It is very gently sloping and is composed of very soft consolidated beach rock flanked on either side by miles of sandy beach. This rock is very easily eroded giving a rough, uneven surface of small pits and projections. This in turn results in a network of small, shallow pools, particularly in the low and middle balanoid.

A subtidal fringe of Plocamium corallorhiza occurs at the bottom of the beach on scattered rock outcrops surrounded by sand. Patella cochlear is absent, probably due to the nature of the substrate as will be discussed. The lower balanoid and "cochlear" zones are dominated by large numbers of the faster growing P.barbara. A dense belt of Caulerpa filiformis in a sandy bottomed gulley separates the lower and middle balanoid zones. Although Tetraclita serrata is abundant, particularly in the middle balanoid, it does not form dense beds due to the easily eroded nature of the substrate. Instead it occurs as scattered clusters of individuals.

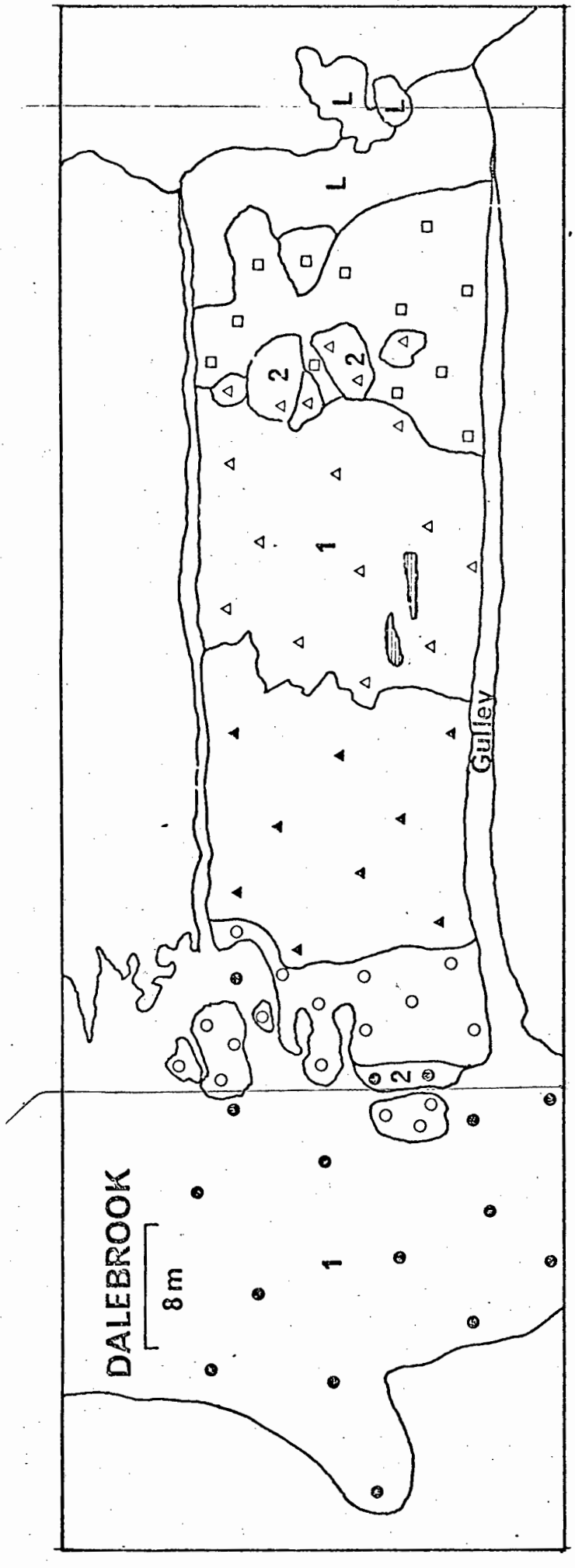


Fig. 1.14

163mm
21mm = 8m
∴ 163 = 62.09m

4km = 15.29m

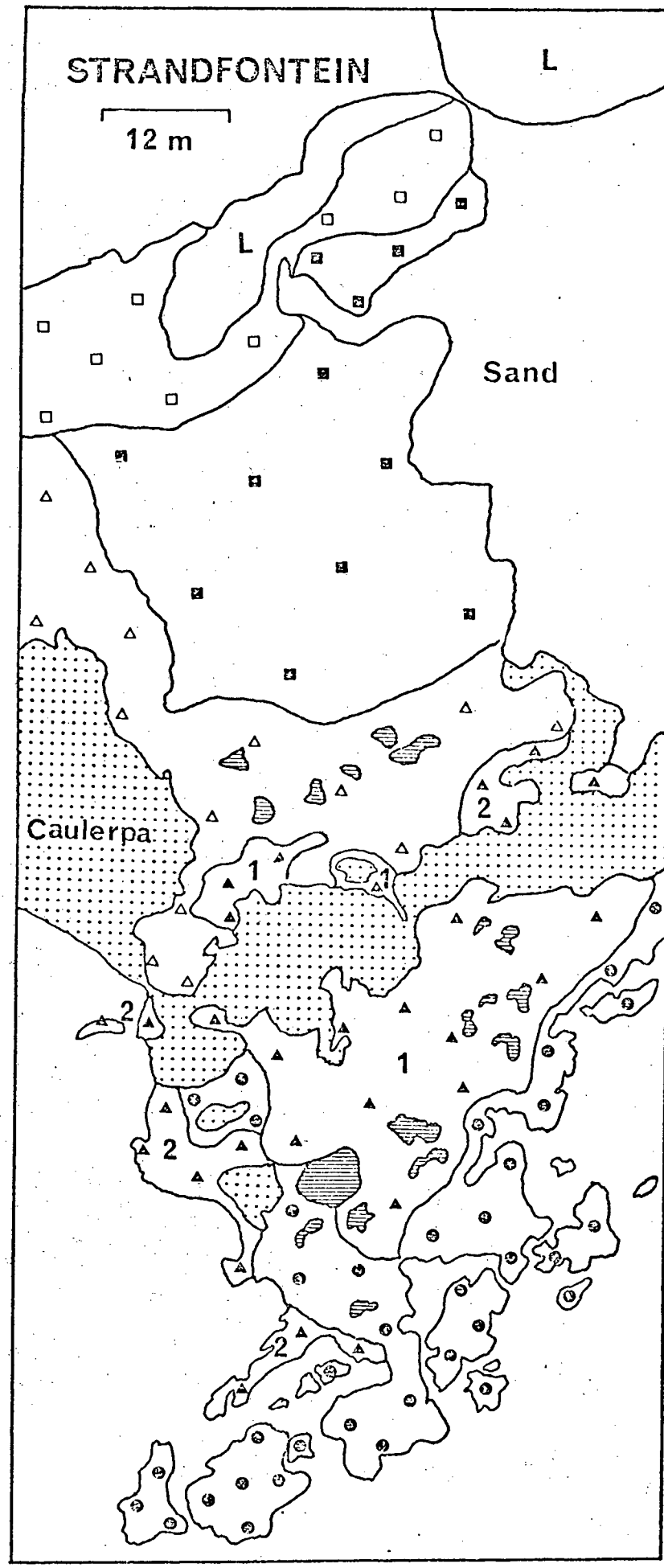


Fig. 1.15

CHAPTER 3 : TRENDS IN TROPHIC COMPARTMENT BIOMASS

INTRODUCTION

Beach communities consist of an array of species which, by their very profusion, make a clear understanding of biotic conditions difficult. In order to gain insight into the functional structure of these communities their complexity may be reduced by examining trophic compartments rather than individual species. Information on the biomass of these compartments may then be considered in terms of :

a) trends in trophic biomass on different beach types;
b) vertical zonation of trophic compartments.

For the purposes of (a) all species were allocated to one of seven trophic compartments (see Tables 1.3, 1.4 in the appendices). Mean biomass $.m^{-2}$ for each beach as a whole was then calculated for each species as described in the similarity analysis section (p.90), allowing characterisation of each beach according to trophic dominance.

In part (b) measured biomass values were used directly to calculate absolute trophic biomass in each zone.

TABLE 1.5 NUMBER OF SPECIES REPRESENTED IN EACH TROPHIC COMPARTMENT

	Exposed Beaches						Sheltered Beaches					
	SPT	OKB	ROB	FPB	DBK	STR	OKA	OFB	KOM	BFA	BFB	FPA
Primary producers	18	9	16	10	24	12	16	19	18	9	3	16
Herbivores	24	16	21	17	31	22	12	23	30	27	20	25
Filter-feeders	7	8	8	20	19	12	2	11	8	9	7	19
Omnivores	4	4	4	2	2	3	0	2	0	2	2	3
Detritivores	7	8	8	6	10	6	2	6	8	5	4	7
Scavengers	18	12	13	16	21	17	9	17	26	20	15	19
Carnivores	20	24	20	27	30	16	3	23	28	20	12	28
T O T A L	98	81	90	98	137	88	44	101	118	90	63	117

TABLE 1.6 : BIOMASS AND PERCENTAGE OF TOTAL BIOMASS FOR TROPHIC COMPARTMENTS.

(Upper figures = biomass ($g.m^{-2}$): Lower figures = Percentage)

	Exposed beaches							Sheltered beaches						
	SPT	ROB	OKB	FPB	DBK	STR	MEAN	OKA	KOM	OFB	BFA	BFB	FPA	MEAN
Primary producers	457,26 81,27	232,12 50,31	297,51 31,01	710,02 33,70	304,17 21,23	197,10 38,30	365,79 36,8	27,67 46,92	233,16 72,56	282,18 85,29	334,68 86,42	35,24 31,16	488,50 89,79	233,57 79,92
Herbivores	37,13 6,60	44,78 9,71	32,43 3,38	26,65 1,25	48,23 3,67	122,23 24,22	51,90 5,13	30,49 51,73	66,12 20,50	45,85 13,86	28,65 7,59	46,78 42,37	17,19 3,02	39,18 13,40
Filter-feeders	43,81 7,79	171,83 37,24	580,19 60,47	1361,22 63,6	1058,34 73,86	172,18 33,46	564,60 55,86	0,34 0,58	15,30 4,76	0,52 0,15	17,27 4,46	9,52 8,42	18,97 3,49	10,32 3,53
Omnivores	6,04 1,07	5,85 1,32	6,86 0,76	13,60 0,12	4,03 0,16	2,37 0,93	6,46 0,64	0,26 0,44	0,00 0,10	0,25 0,02	0,27 0,55	0,03 4,96	0,14 1,07	0,16 0,06
Detritivores	4,42 0,79	0,39 0,03	0,37 0,003	2,65 0,12	2,25 0,09	4,78 0,02	2,48 0,24	0,04 0,07	0,31 0,10	0,07 0,02	2,12 0,03	5,61 0,24	5,84 0,17	2,33 0,80
Scavengers	7,60 1,35	1,28 0,28	8,86 0,92	13,92 0,65	6,97 0,49	1,84 0,36	6,75 0,67	0,14 0,24	5,30 1,65	1,53 0,46	2,49 0,64	10,52 9,30	8,50 1,56	4,75 1,62
Carnivores	6,35 1.13	5,10 1.11	33,18 3.46	11,81 0,55	7,11 0,50	13,95 2,71	12,92 1,28	0,01 0,02	1,07 0,33	0,47 0,14	1,19 0,31	4,08 3,61	4,92 0,90	1,96 0,67
TOTAL	562,60 100	461,36 100	959,40 100	2139,87 100	1432,86 100	514,63 100	1010,90 100	58,94 100	321,27 100	330,88 100	387,25 100	113,08 100	544,06 100	292,27 100

(a) TRENDS IN TROPHIC BIOMASS

An important point revealed by this analysis which will be reiterated in the following sections is that each compartment is often dominated in terms of biomass, by one or only a few species. Trends in trophic biomass thus tend to reflect biomass trends in these major species. Furthermore there is generally no correlation between the number of species present in each compartment (Table 1.5) and the actual biomass of that compartment (Table 1.6).

Two further preliminary points are obvious : Firstly, from Table 1.6 it can be seen that total biomass is markedly low for the two boulder beaches OKA and BFB due to instability of substrate. A t-test between total biomass of these and remaining beaches indicates biomass to be significantly lower on the former ($P < 0,01$). This reduction in biomass is most obvious for the algae, in agreement with the findings of Isaac (1937) that algae are least dense on beaches formed from small boulders. Algae are extremely sparse on these two beaches and no subtidal algal fringe occurs. Similarly the sedentary filter-feeders are greatly impoverished in both richness and biomass (see below). It is noticeable however that the abundance of more mobile herbivores remains similar to that of other beaches.

Secondly, total biomass is significantly higher for exposed than sheltered beaches (Table 1.7). Froggy Pond A has an unusually high average biomass for a sheltered beach due largely to the extensive and very dense bed of Bifurcaria brassicaeformis fringing the beach. Algae at FPA form 90,62 % of total biomass (the highest value for all beaches) and are so abundant as to raise mean total biomass.

Analysis of variance to test for further trends in trophic biomass is inappropriate as not all possible combinations of factors exist and therefore t-tests were carried out on each compartment. t-tests were used to compare mean biomass of :

warm vs. cold beaches, exposed vs. sheltered beaches

granite vs. TMS beaches, granite vs. Malmesbury shale beaches

and shale vs. TMS beaches.

TABLE 1.7 : VALUES OF P DERIVED FROM t-TESTS BETWEEN MEANS OF TROPHIC BIOMASS

Trophic Compartment	COMPARISON		
	Warm/cold	Exposed/ Sheltered	Igneous/ Sedementary
Primary producers	> 0,05	> 0,05	> 0,05
Herbivores	> 0,05	> 0,05	> 0,05
Filter-feeders	> 0,05	< 0,01	> 0,05
Omnivores	> 0,05	< 0,01	> 0,05
Detritivores	> 0,05	> 0,05	> 0,05
Scavengers	> 0,05	> 0,05	> 0,05
Carnivores	> 0,05	< 0,05	> 0,05
Total biomass	> 0,05	< 0,05	> 0,05

Of all these tests the only significant differences were found in exposed vs. sheltered comparisons (Table 1.7). Filter-feeders and omnivores showed differences at 99 % confidence level and carnivores at 95 % level. In all three cases biomass was higher for exposed beaches.

It is clear that exposed and sheltered beaches differ in biomass of different trophic compartments. Thus although species composition may differ considerably on different beaches there appear to be two main "functional types" of beach revealed when the community is defined in terms of trophic compartment biomass.

Sheltered beaches

Excluding the two boulder beaches, (Oudekraal A and Buffels Bay B), sheltered beaches are dominated, in terms of biomass, by primary producers which form between 70 and 90 % of total biomass. On the two boulder beaches algae form only approximately 30 % of total biomass. On the remaining sheltered beaches, mean algal biomass is in the region of 200-300 g $.m^{-2}$. The extensive, dense subtidal weed bed of Froggy Pond A results in a higher mean biomass for this beach.

Herbivores form the most abundant faunal component. While biomass of these is relatively more variable than of algae, values are generally between 20 and 50 g $.m^{-2}$, the highest being at Kommetjie (66 g $.m^{-2}$). Despite lower total biomass values the two boulder beaches do not have depressed herbivore biomass. Consequently herbivores form a larger percentage of total biomass.

The biomass of filter-feeders is markedly low for sheltered beaches, averaging only 7,23 g $.m^{-2}$. This is presumably due to decreased feeding efficiency in less turbulent conditions.

Carnivore biomass is also particularly low for sheltered beaches, due possibly, to association with filter-feeders (see below, p.82). Scavengers, omnivores and detritivores form minor trophic compartments in decreasing order of abundance. Biomass is low for all three of these but significantly lower for omnivores on sheltered than exposed beaches. This again is due in part to association with filter-feeders as will be discussed below.

Sheltered beaches are thus generally dominated by algal and herbivore populations. Filter-feeder biomass is low but, with the exceptions of Olifantsbos and Buffels Bay B, forms the third most abundant component. Carnivore biomass is also low and scavengers are more abundant on most of the sheltered beaches. Omnivores and detritovores form a low percentage of total biomass.

Exposed beaches

Filter-feeders form a much larger proportion of exposed beach biomass and at three of these, Oudekraal B, Froggy Pond B (FPB) and Dalebrook (DBK), become the most abundant trophic compartment overshadowing even the algae.. Biomass of filter-feeders is extremely high at some beaches (eg. 1361 g $.m^{-2}$ at FPB and 1058 g $.m^{-2}$ at DBK), dominating the entire community.

Algae show no significant difference in biomass compared with sheltered beaches and are of similar levels. Likewise herbivores, which now become the third most abundant component tend to be of similar abundances as on sheltered beaches except that the value for Strandfontein is particularly high (172 g $.m^{-2}$, see below p.77).

Carnivores are significantly more abundant and on most exposed beaches rank before scavengers in abundance. Omnivores are also significantly more abundant and on exposed beaches are almost as abundant or more so than scavengers. Detritivores still form a relatively minor component of these communities.

To summarise, exposed beaches are dominated by filter-feeders and algae, in contrast to sheltered beaches. Herbivores, although at similar abundances as on sheltered beaches form a smaller percentage of overall biomass on exposed beaches. Carnivores are generally more abundant than scavengers and omnivores attain similar or higher values than the latter. However these minor trophic compartments still form only a small fraction of total biomass.

Within the framework of these two basic types each beach has its own peculiarities. The main variations are mentioned below.

Seapoint conforms to the basic exposed pattern but has a noticeably lower filter-feeder biomass than other exposed beaches. This is largely due to the unusually low biomass of the important barnacle Tetraclita serrata on the upper shore.

Strandfontein an exceptionally high herbivore biomass is found here, formed largely (75-87 %) by Patella barbara. This is thought to be a consequence of unusual substrate conditions (see below, p.126). Although filter-feeder biomass is quite high the dense beds of barnacles found on other exposed beaches do not occur here. This too is thought to be an effect of the very soft substrate.

In order to gain a better understanding of these trophic compartments and the trends they show in response to varying physical parameters, each compartment can now be examined in greater detail.

1. Primary producers

Biomass of this compartment is particularly low for the two boulder beaches (OKA and BFB) due to substrate instability as described above (p.47). Strandfontein has a relatively low biomass. The extensive Littorina, upper and middle balanoid zones are all virtually devoid of algae. Also there is a relatively low biomass in the lower balanoid, except where Gelidium pristoides forms a separate sub-zone. The low algal biomass is thought to be due to a sand-scouring effect as the rock is surrounded by sandy beaches. A similar effect is described by Daly and Mathieson (1977). The extremely friable nature of the substrate (consolidated beach rock) is an additional impediment to algal growth. Unsuitability of substrate thus accounts for low algal biomass on these three beaches.

On the remaining beaches lower biomass is found on the two beaches which lack a distinct sub-tidal weed fringe, Kommetjie and Robben Island, on both of which a merged cochlear/weed zone occurs. (Note that a fringe is also missing from OKA and BFB). A sub-tidal fringe is not only a source of great species richness, it also makes a very important contribution to total primary producer biomass.

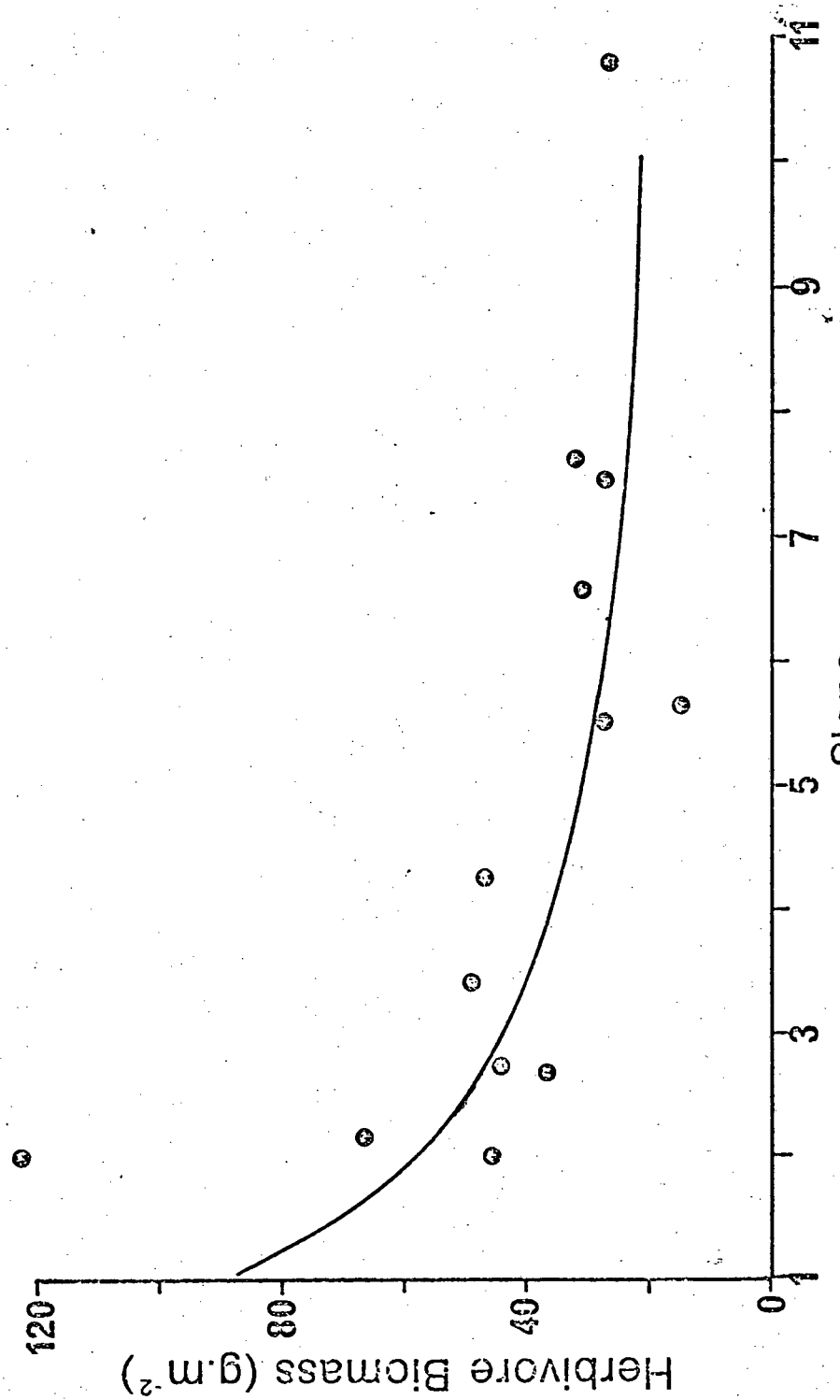


Fig. 1.16 The relationship between beach slope or inclination (derived as Δ H/ Δ L) and herbivore biomass ($y=92,19x^{-0,65}$; $r=0,72$)

Although the fringe at Dalebrook is less dense than all others, it is very extensive. Algal density in the lower balanoid is high here and these two points result in a mean algal biomass comparable to the other beaches.

Despite the observation by Levyns (1924) that Table Mountain Sandstone forms a much more favourable substrate for algae than granite no significant difference was found between the biomass of algae on different rock types (Table 1.7). Similarity analyses based on data for algae alone show no grouping of beaches on the basis of substrate (see Chap. 4).

2. Herbivores

Fig. 1.16 shows a graph of total herbivore biomass $.m^{-2}$ versus beach inclination and suggests a correlation between these two factors. Ranking these beaches according to herbivore biomass indicates that they may be divided into four groups, in order of decreasing biomass: (Table 1.8)

1. Strandfontein, Kommetjie, Dalebrook and Olifantsbos.
2. Robben Island and Seapoint.
3. Oudekraal B, Buffels Bay A, Froggy Pond A and Froggy Pond B.
4. Oudekraal A and Buffels Bay B.

Highest herbivore biomass $.m^{-2}$ occurs in groups 1 and 2, which are all gently sloping beaches, and these two together show a significantly higher herbivore biomass than group 3 ($P<0,05$). Although groups 1 and 2 do not have significantly different means for herbivore biomass ($P>0,05$) the two ridged Malmesbury shale beaches of group 2 do have intermediate values which are significantly higher than those of group 3 ($P<0,05$).

Group 3 consists of very steep beaches made up of huge granite boulders and herbivore biomass $.m^{-2}$ is lowest for this group. Although BFA is a Table Mountain sandstone beach it too is composed of huge boulders with steeply sloping or vertical faces.

TABLE 1.8 : PERCENTAGE COMPOSITION OF HERBIVORE BIOMASS

Group I	*Patella* spp.	*Siphonaria* spp.	*Oxystele* spp.	Total	Most abundant herbivore species in decreasing order
OFB	87,52	5,37	2,68	95,57	*P.cochlear*
KOM	82,35	10,08	0,29	92,72	*P. granatina*
DBK	58,66	6,45	23,25	88,39	*O.variegata*, *P.cochlear*
STR	84,67	3,09	4,86	92,62	*P.barbara*, *P. granularis*
Group II					
ROB	86,06	4,94	0,36	91,36	*P. cochlear*
SPT	77,28	0,88	14,14	92,31	*P.granularis*, *P.cochlear*
Group III					
OKB	75,86	0,38	5,18	81,42	*P.granularis*
BFA	45,56	1,28	31,52	78,36	*P.barbara*, *P. oculus*, *O.variegata*, *P.cochlear*
FPA	73,45	0,47	12,36	86,28	*P.barbara* *P.cochlear*
FPB	69,93	1,22	12,77	83,92	*P.granularis*, *P.barbara*
Group IV					
OKA	80,34	14,89	0	95,23	*P.cochlear* *P.granularis*
BFB	30,65	0	47,93	78,58	*O.variegata*, *P.oculus*

Oudekraal A and Buffels Bay B may be included into groups 3 and 1 respectively on the basis of herbivore biomass $.m^{-2}$. These two beaches are however generally aberrant as they offer unstable substrates. The composition of herbivore biomass does not conform to the pattern evident for the remaining beaches and they are therefore classified into a separate group.

A correlation thus exists between beach shape and herbivore biomass. Although 49 species are included in this trophic compartment many of them are small species such as amphipods etc. On all beaches the bulk of herbivore biomass (78 - 95 %) is formed by Patella spp. Oxystele spp. and Siphonaria spp. Examination of table 1.8 reveals several important points.

1. The percentage of herbivore biomass formed by Patella spp. is greater in groups 1 and 2 together than in group 3 ($P < 0,05$). Note however that at Dalebrook a large population of O. variegata detracts from the significance of the Patella spp. Buffels Bay B and Oudekraal A (group 4) are both boulder beaches and Patella spp. are not very abundant on either. At BFB the more mobile Oxystele variegata is very abundant so that overall herbivore biomass remains high. At OKA however O. variegata is not abundant so that although Patella spp. biomass is low it still forms the bulk of herbivore biomass.

2. Siphonaria spp. are most important in group 1 ($P < 0,05$). This is also indicated by the fact that separate Siphonaria zones occur only on beaches in group 1.

In group 2 Robben Island has recognisable Siphonaria pools (though not a separate Siphonaria zone) and Siphonaria spp. are more important here than at Seapoint. Siphonaria spp. are of very limited significance in group 3.

To summarise, the long flat beaches (group 1) have a higher herbivore biomass and are generally dominated (in terms of herbivore biomass) by Patella spp., particularly P. cochlear and P. granatina. Where substrate is unsuitable for P. cochlear (at Strandfontein) it is replaced by P. barbara.

Beaches in Group 2 are intermediate in having a moderate biomass of herbivores and Patella spp. are still the most abundant herbivores. These are the two Malmesbury shale beaches which, though still broad and gently sloping, have a very characteristic form due to the weathering of this rock type. (see above). At Robben Island P. cochlear is the most abundant Patella species and an extensive and heterogenous cochlear zone occurs as described above. At Seapoint P. cochlear is second in abundance to P. granularis, due to both the restricted nature of the cochlear zone, which is encroached on by the Bifurcaria zone in its lower reaches, and to the extensive lower and upper balanoid zones where P. granularis is abundant, particularly in the upper balanoid.

Group 3 is composed of beaches consisting of huge boulders so that the lower zones particularly tend to be much steeper and thus narrower than on the other beaches. Herbivore biomass is lowest for this group and the contribution of Patella spp. is generally reduced. P. cochlear becomes less important here as the cochlear zone is more restricted and other species of this genus (especially P. barbara and P. granularis) become more important. O. variegata makes a greater contribution and Siphonaria spp. decline completely in significance, due to the absence of suitable flat stretches of rock on the upper beach.

Although densities of Patella spp. and O. variegata within the zones they occupy tend to be higher for groups 1 and 2, the effect of beach shape on overall herbivore biomass is partially due to its influence on the width of zones. On very steep beaches the lower zones in particular tend to be very narrow. Consequently although the density of herbivores within these zones may be moderately high their contribution towards total biomass of the beach is reduced.

Finally it is important to note that a correlation between herbivore and macroalgal biomass is not implied. Many of the major herbivores feed on lichens or diatom films (eg. Patella granularis, P. granatina (Branch, 1971), Siphonaria spp.,(pers. obs.) or on encrusting algae such as Ralfsia spp. or Lithothamnion spp. (eg. P. cochlear, P. longicosta, (Branch, 1974)).

3. Filter-feeders

Biomass values for filter-feeders were shown above (p. 46) to be significantly higher for exposed beaches ($P < 0,01$). As with other trophic compartments this is not correlated with a greater number of species. For example although Froggy Pond A has the third highest number of species in this compartment (Table 1.5), it has a very low biomass of filter-feeders (Table 1.6). Biomass is particularly high for Froggy Pond B (which has extremely dense beds of Octomeris angulosa) and Dalebrook (where dense beds of Pyura stolonifera and of Tetraclita serrata occur). The high value at Oudekraal B is due mainly to the presence of Aulacomya ater and O. angulosa plus some T. serrata in the upper balanoid.

Increased filter-feeder biomass on exposed beaches has also been found by Southward and Orton (1954) and Jones and Demetropoulos (1968) and is probably associated primarily with greater water movement, facilitating feeding. Octomeris angulosa was found both in the present work and in that of Field and MacFarlane (1968) to be a good indicator of exposed conditions (see below).

Filter-feeders are particularly important as they completely dominate exposed shores and on some beaches even exceed algae in biomass. Such abundance of one particular trophic compartment has a profound effect on the community as a whole. Not only do filter-feeders compete with other forms for space but they also offer a varied and complex micro-environment for smaller species of crustaceans etc.

Even when present at low biomass many of the major filter-feeder species tend to form very dense populations ranging from small, scattered clumps to huge sheet-like populations on exposed beaches. This is due to the gregarious habit of the larvae, which are induced by the presence of adult forms to settle where others of the same species (or in some cases other species) are already present (Knight-Jones and Stevenson, 1950; Crisp and Knight-Jones, 1953; Knight-Jones, 1953; Wilson, 1968; Larman and Gabbott, 1975). Filter-feeders thus cause both structural and functional differences to communities when present at high biomass.

On ranking beaches according to the total number of filter-feeder species present, there is no correlation with actual biomass. With the exception of the two Buffels Bay beaches (BFA/BFB) however warm beaches show a significantly higher number of species than cold beaches ($P < 0,01$). This is presumably due to overlap of the west and south coast biota in False Bay (see below). The low number of species at Buffels Bay may be due to sudden and severe changes in water temperature caused by tongues of cold water which extend around Cape Point into False Bay as far as Buffels Bay, resulting in a lowered number of species. Filter-feeder richness at BFB as at OKA, is particularly low as this is a boulder beach with low overall richness as described.

4. Carnivores

This compartment also shows significantly higher biomass on exposed beaches ($P < 0,05$). Again higher biomass is not associated with a greater number of species. Carnivore populations are composed of both species which may prey directly on filter-feeders (eg. whelks such as Thais dubia) and smaller species such as errant polychaets, pycnogonids etc. It seems likely that these smaller carnivores feed on small crustaceans etc. which may be more abundant in the various microhabitats offered by filter-feeder populations. Thus increased carnivore biomass on exposed beaches may be due in part to association with increased filter-feeder biomass. This is brought out in more detail in the section on zonation of trophic compartments (see below).

5. Omnivores

The omnivore compartment contains a small number of species which are mostly of dubious trophic status. t-tests indicate a significant difference between omnivore biomass $.m^{-2}$ of exposed and sheltered beaches. However the errant polychaete Pseudonereis variegata forms a large percentage of omnivore biomass on most beaches (Table 1.9). Trends in omnivore biomass are thus dominated by trends of biomass for P. variegata. This species is most common among algal tufts or in clumps of mussels or barnacles (Day, 1969) and shows significantly higher biomass on exposed beaches ($P < 0,01$). If P. variegata is omitted from this trophic compartment no significant trends are revealed in omnivore biomass.

TABLE 1.9 : PERCENTAGE OF TOTAL OMNIVORE BIOMASS FORMED BY PSEUDONEREIS VARIEGATA

	Exposed beaches						Sheltered beaches					
	SPT	OKB	ROB	FPB	DBK	STR	OKA	KOM	OFB	BFA	BFB	FPA
Tot. Omnivore biomass ($g .m^{-2}$)	6,04	6,86	5,85	13,60	4,03	2,37	0,25	0	0,25	0,27	0,03	0,14
% formed by P.variegata	99,78	98,20	95,05	88,46	100	75,68	100	0	91,96	100	100	37,14

6. Detritivores

This compartment is also dominated in terms of biomass by a single species, the urchin Parechinus angulosus (Table 1.10). Although P. angulosus is included in this compartment for convenience it is not a true detritivore in the usual sense. Juveniles do feed largely on detritus but adults feed primarily on large pieces of algal debris (Greenwood pers. com. 1979).

The only cold water beach showing a large detritivore biomass is Seapoint, again formed largely (91,44 %) by P. angulosus. If Seapoint is omitted from a comparison of omnivore biomass on cold and warm beaches, they are found to differ at 99 % significance. Again this reflects a trend in biomass of one particular species.

The absence of P. angulosus from the warm beach Froggy Pond B is due to the absence of pools and the very steep slope of this granite beach. Although Froggy Pond A is also a granite beach it is much flatter in its lower reaches and P. angulosus occurs in the subtidal fringe.

TABLE 1.10 : PERCENTAGE OF DETRITIVORE BIOMASS FORMED BY PARECHINUS ANGULOSUS

	Cold beaches						Warm beaches					
	SPT	OKA	OKB	ROB	OFB	KOM	BFA	BFB	FPA	FPB	DBK	ST
Tot.Detritivore biomass ($g .m^{-2}$)	4,42	0,04	0,37	0,39	0,07	0,31	2,12	5,61	5,84	2,65	2,25	4,
% formed by P.angulosus	91,44	0	91,70	62,86	0	0	95,06	99,51	84,48	0	45,58	98,

Finally no trends were apparant for scavenger biomass on different beach types. No correlation was shown with exposure, temperature, substrate, beach form or the abundance of other tophic compartments.

(b) ZONATION OF TROPHIC COMPARTMENTS

The component species of each trophic compartment may be expected to have broadly similar biological requirements. Physical conditions alter in different regions of the beach influencing species presence and thus biological interactions. Trophic compartment biomass may thus be expected to reflect changes in physical conditions. For example intertidal algae may be limited by desiccation and high light intensities in the upper regions or low light intensities in the lower regions. Similarly filter-feeders may be restricted by the duration of submergence and thus feeding time in a particular region, or by competition for primary space with algae and so on. In order to examine the effects of vertical height on the various trophic compartments the biomass for each compartment was calculated for each of the zones recognised. In contrast to the previous section the data used in these calculations are derived from measured biomass for each zone and not mean biomass for the whole beach. For the purposes of this analysis rock-pools were omitted as they interfere with general trends in conditions up the beach.

For convenience the basic type of beach shape for each substrate are shown schematically in fig. 1.17. Figs. 1.18 - 1.29 show the zonation of trophic compartments on each beach. A number of trends are discernible.

1. Primary Producers

Algal biomass is generally maximal at the bottom of the shore although areas of high algal biomass occur in the upper regions when Porphyra capensis is present. Desiccation and high light intensities, to which algae are very susceptible (Levyns, 1924) in conjunction with herbivore grazing pressure are probably the main limiting factors towards the top of the shore. Porphyra however can withstand prolonged periods of drying and may thus colonise much higher regions. Although algae and filter-feeders may compete for primary space (eg. Paine, 1971a) such competition is likely to limit mainly the latter. Not only can algae utilise filter-feeders as a substrate but their fronds are likely to produce a

Fig. 1.17 Schematic representation of beach profiles for different rock types.

Although local topography is obviously important the major rock types show the following general weathering forms:

Granite - huge exhumed boulders forming very steep rock faces.

Table Mountain Sandstone - flat, gently sloping beaches, sometimes steplike due to weathering in large blocks.

Malmesbury Shale - again fairly flat but characterised by long parallel ridges formed because of tilting of the bedding planes. These ridges run perpendicular to the sea.

In addition there are beaches formed from much softer consolidated beach rock along the north coast of False Bay. These are wide and extremely gently sloping.

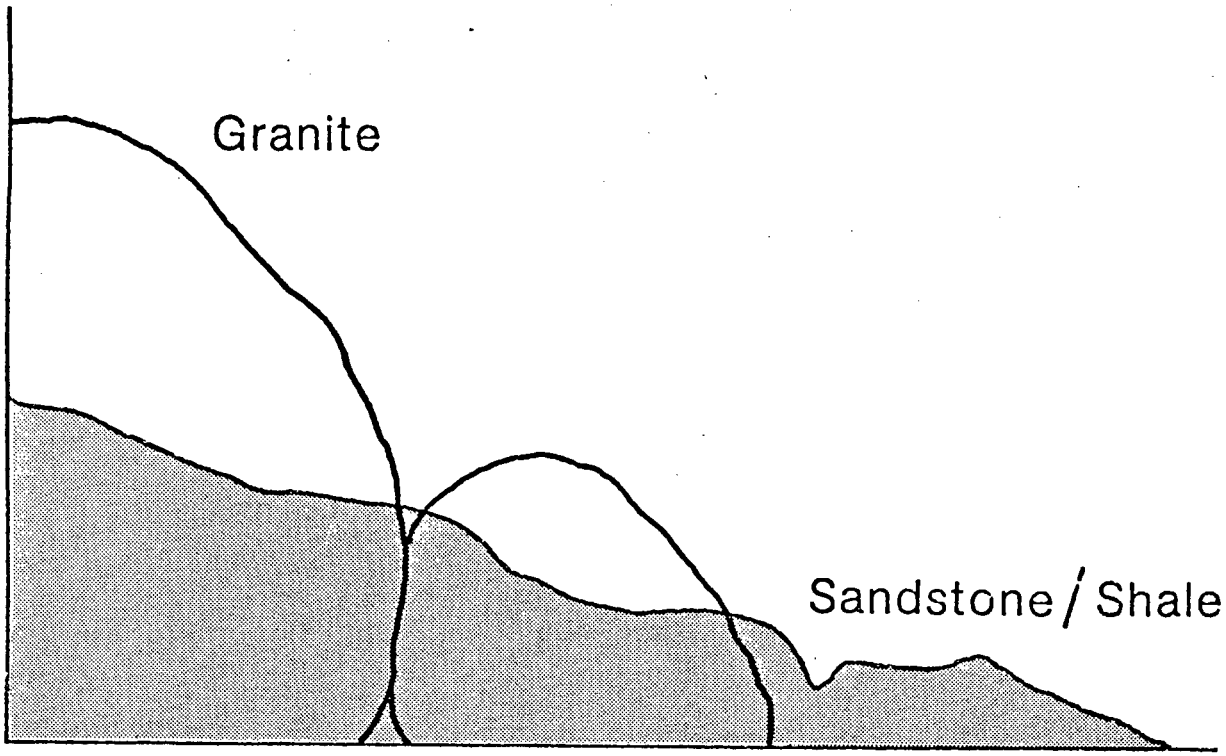


Fig. 1.17

Figs. 1.18 - 1.29. Profile diagrams of 12 beaches examined showing biomass of the seven trophic compartments considered.

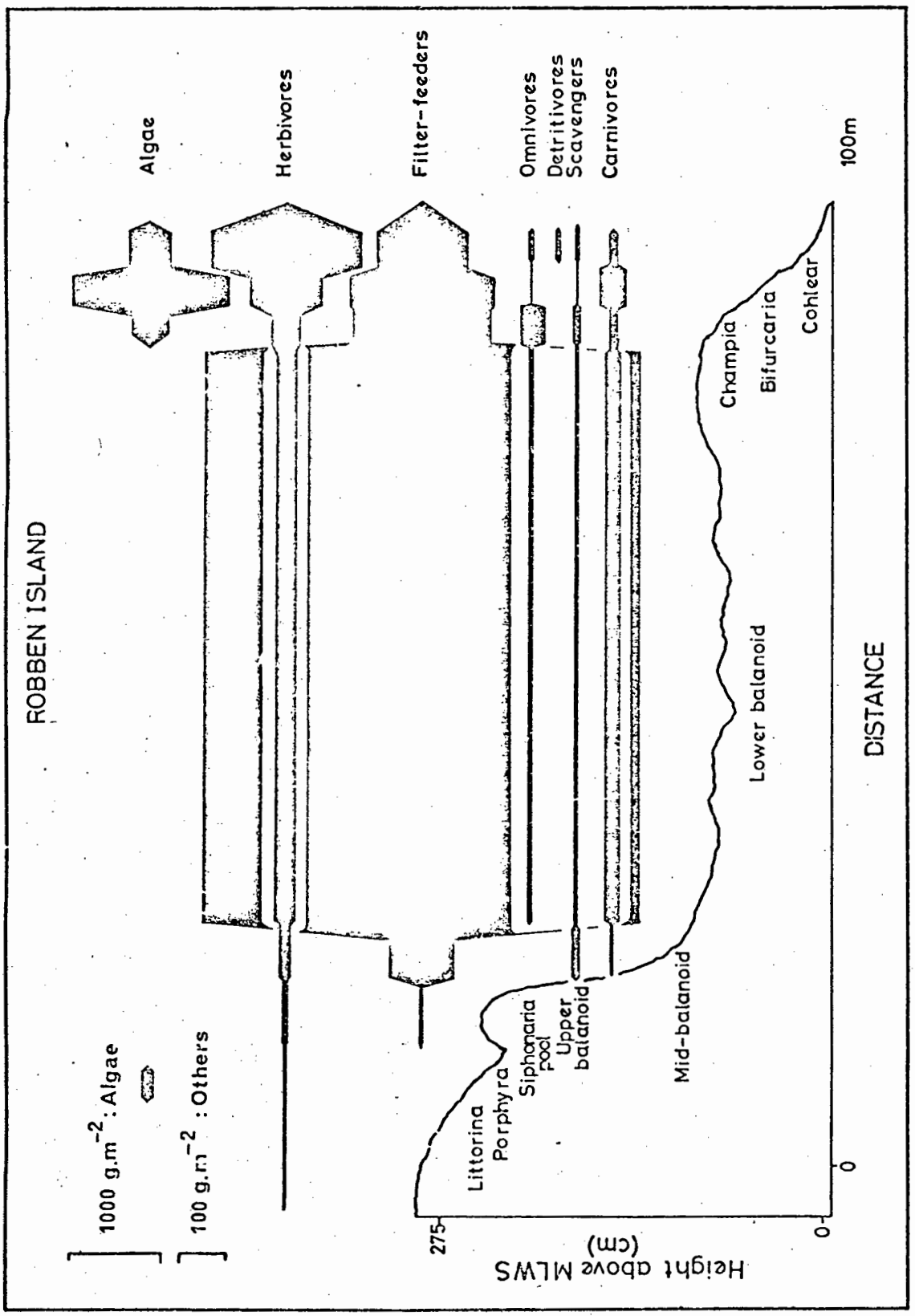


Fig. 1.18 Profile diagram of Robben Island.

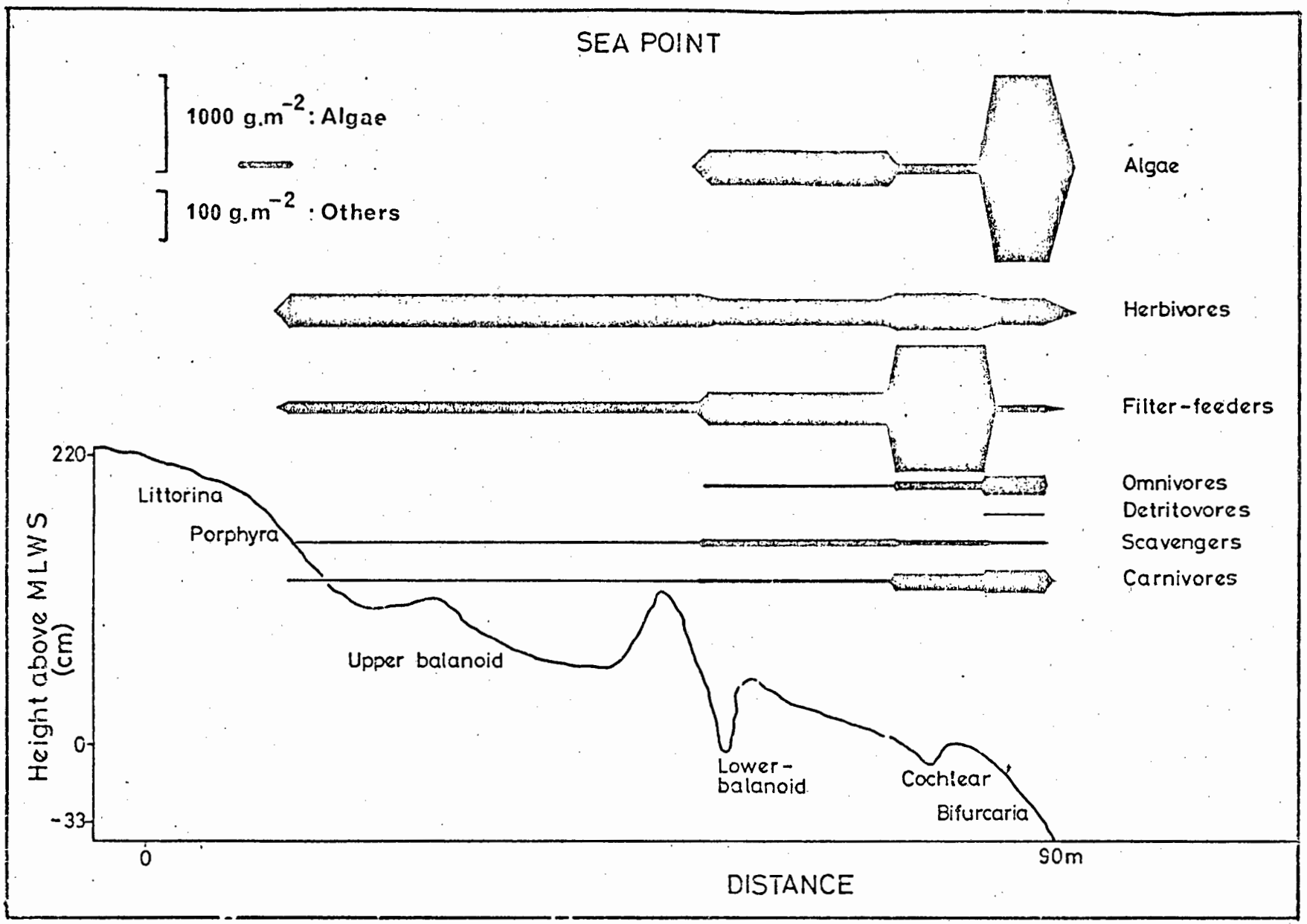


Fig. 1.19 Profile diagram of Sea Point.

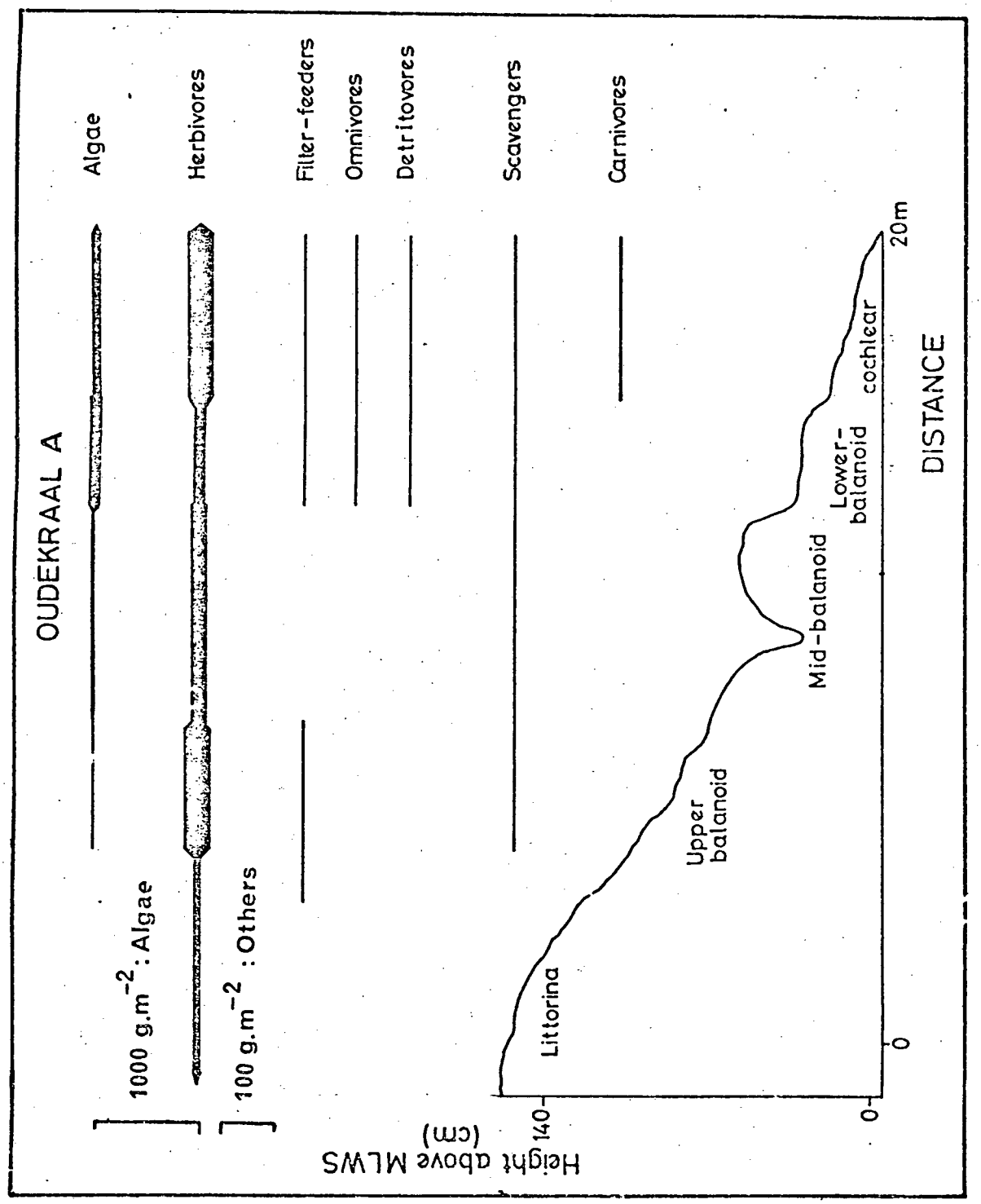


Fig. 1.20 Profile diagram of Oudekraal A.

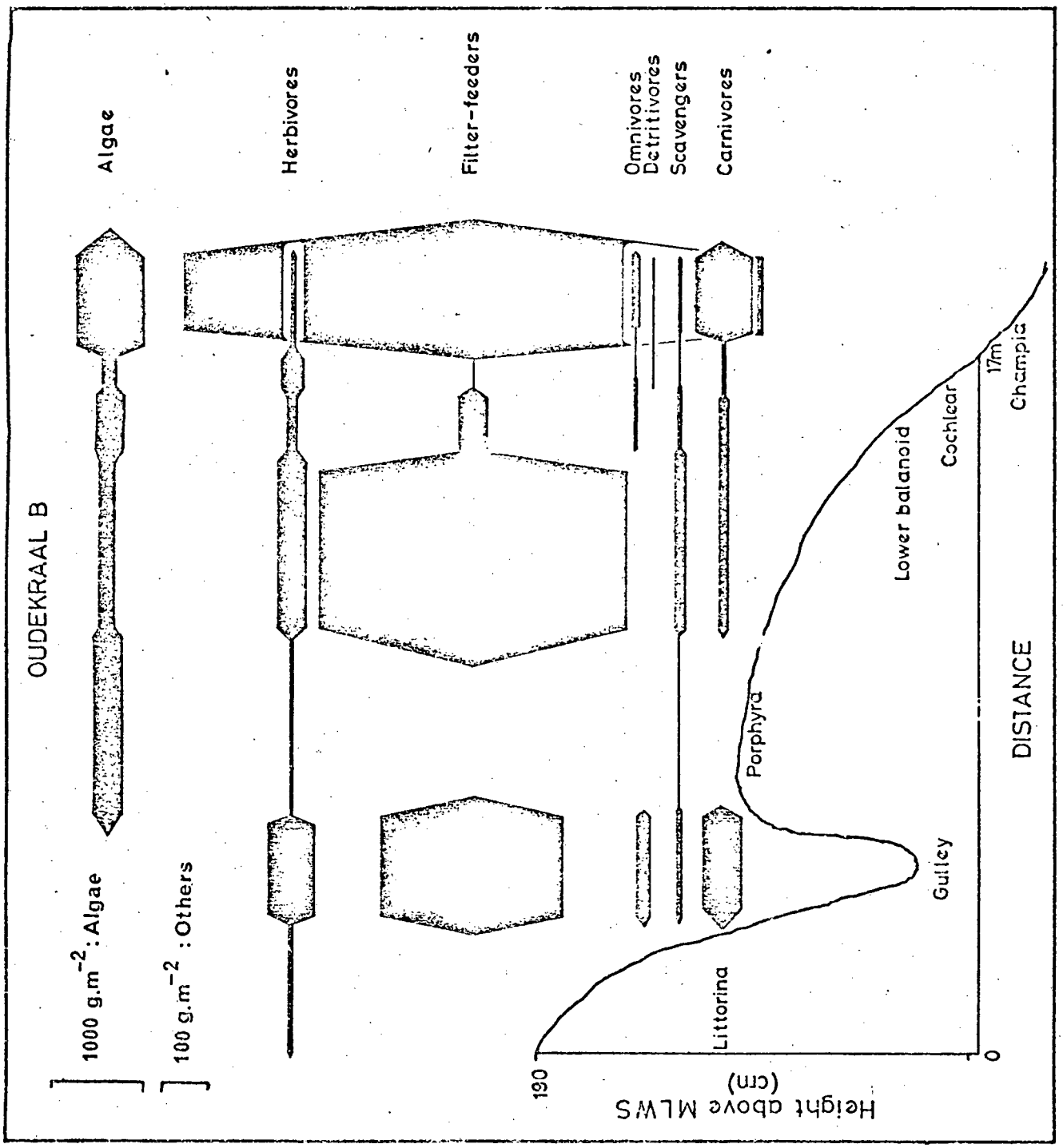


Fig. 1.21 : Profile diagram of Oudekraal B.

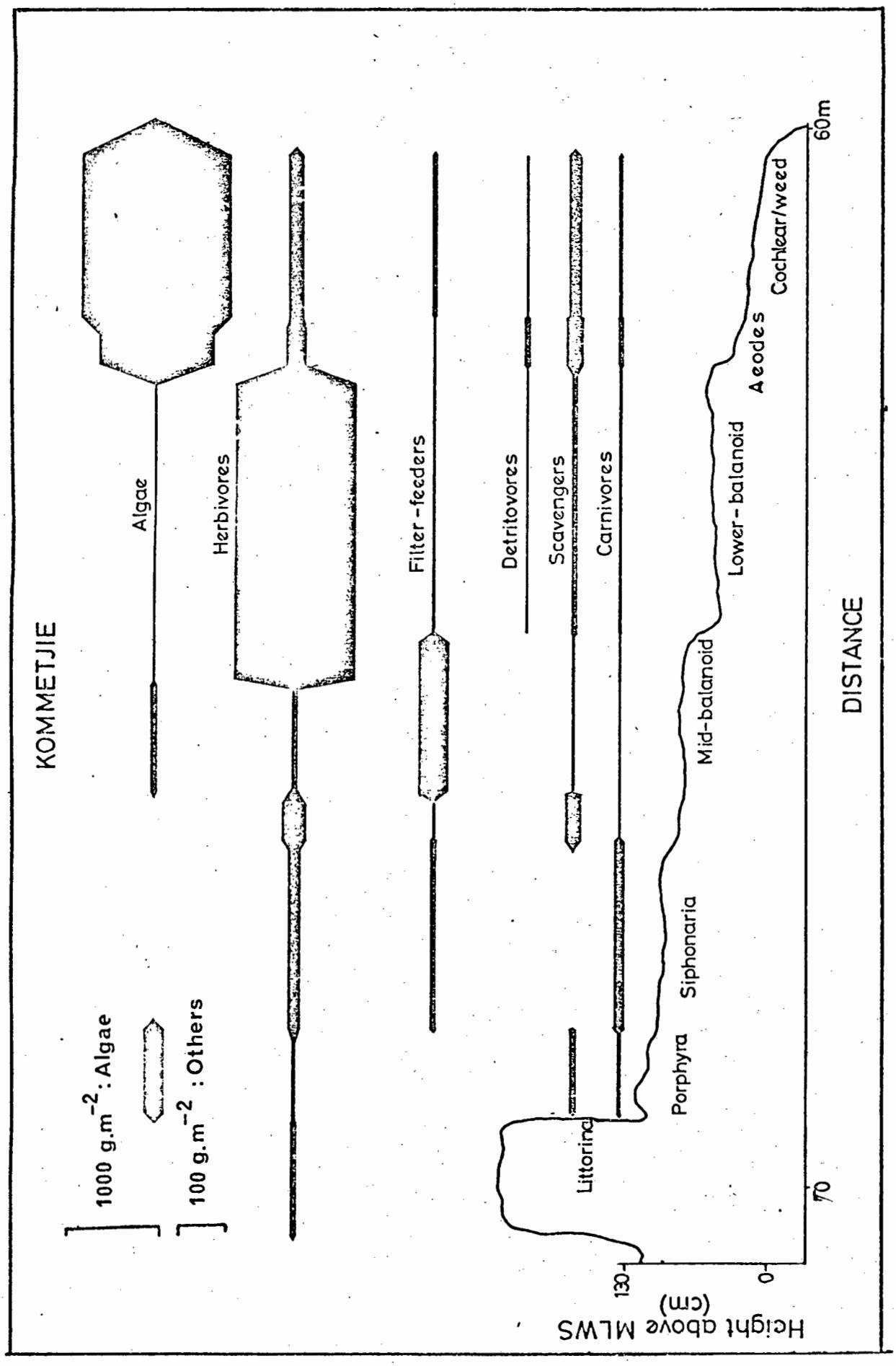


Fig. 1.22 Profile diagram of Kommetjie.

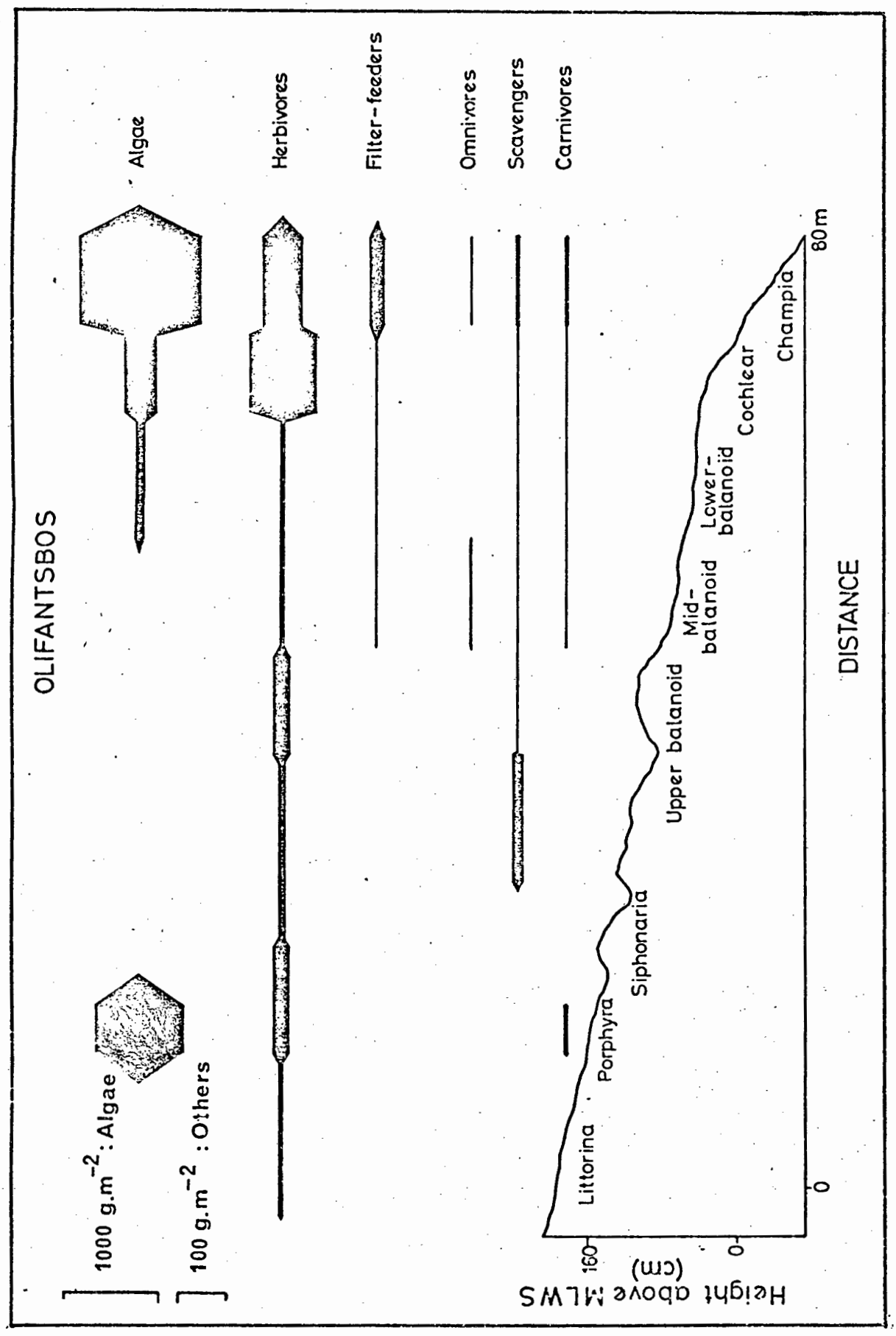


Fig. 1.23 Profile diagram of Olifantsbos

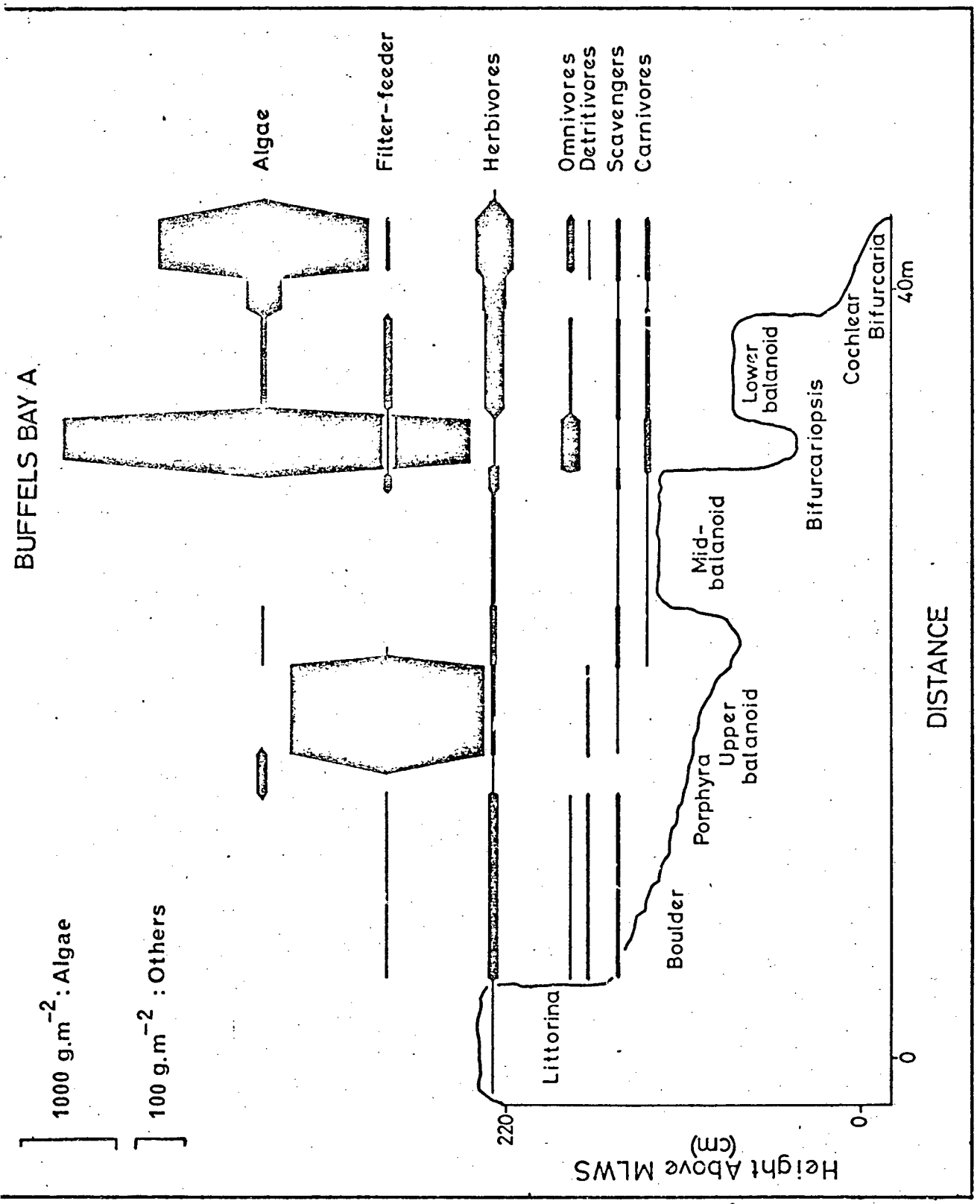


Fig. 1.24 Profile diagram of Buffels Bay A.

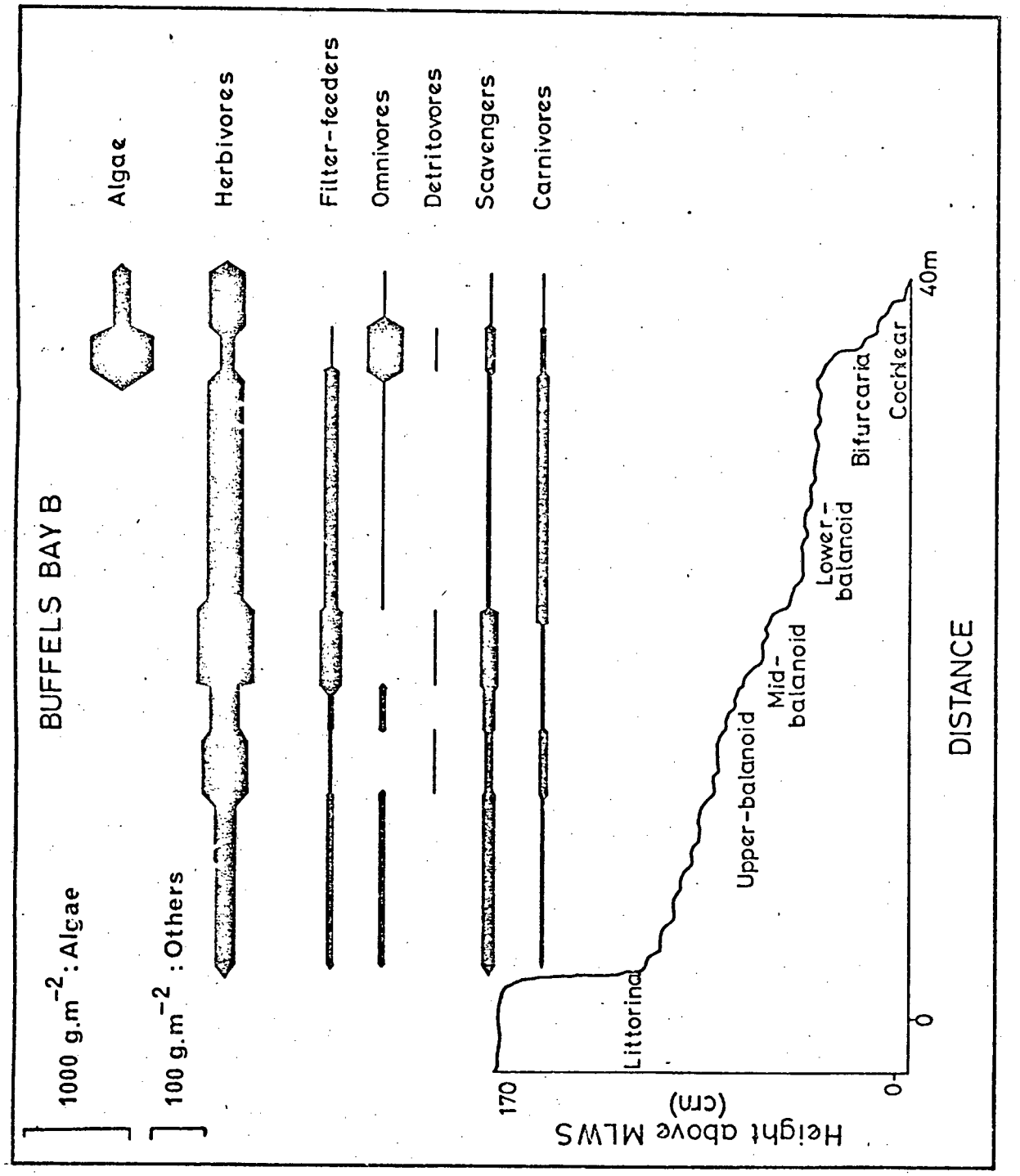


Fig. 1.25 Profile diagram of Buffels Bay B.

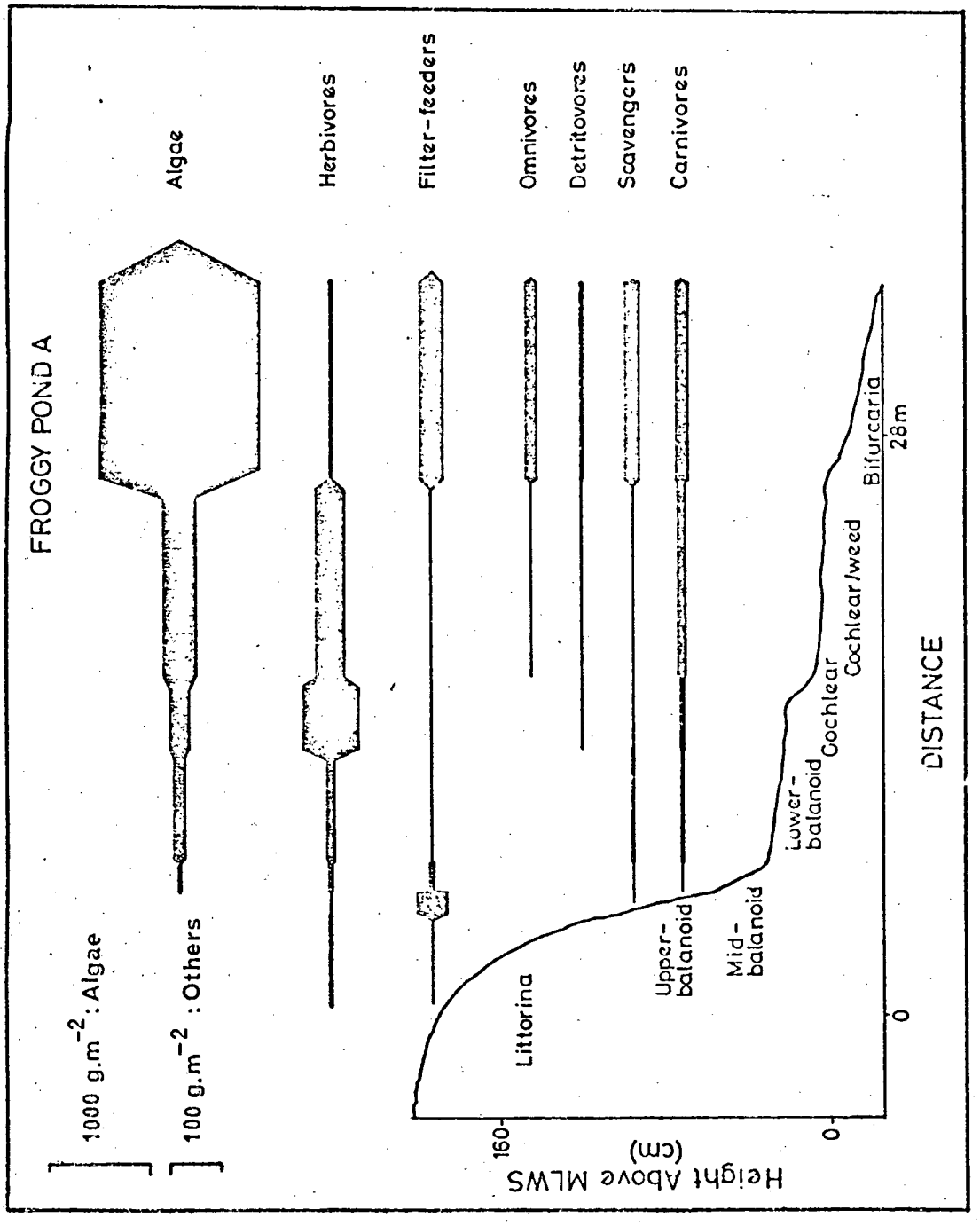


Fig. 1.26 : Profile diagram of Froggy Pond A.

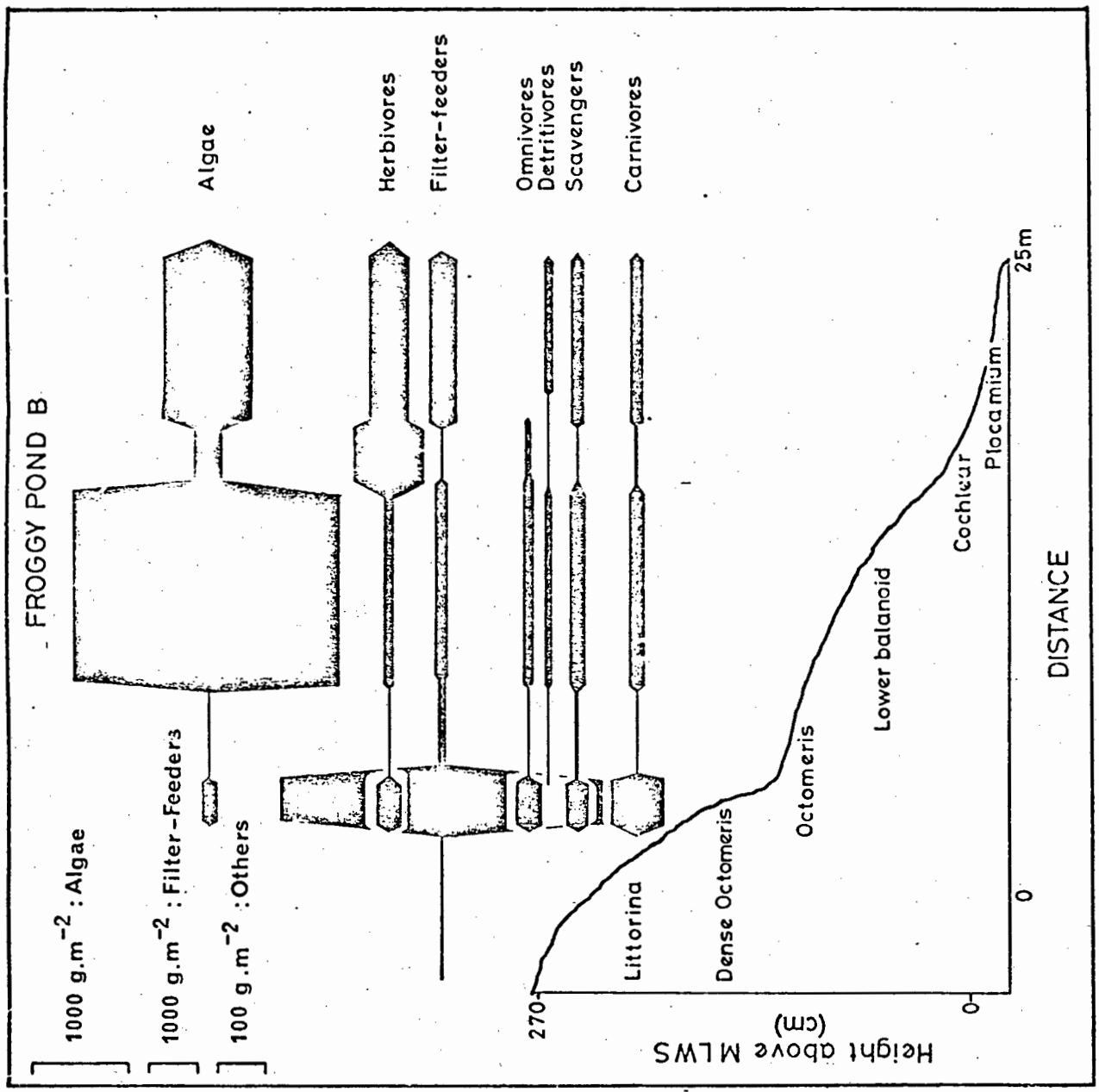


Fig. 1.27 Profile diagram of Froggy Pond B.

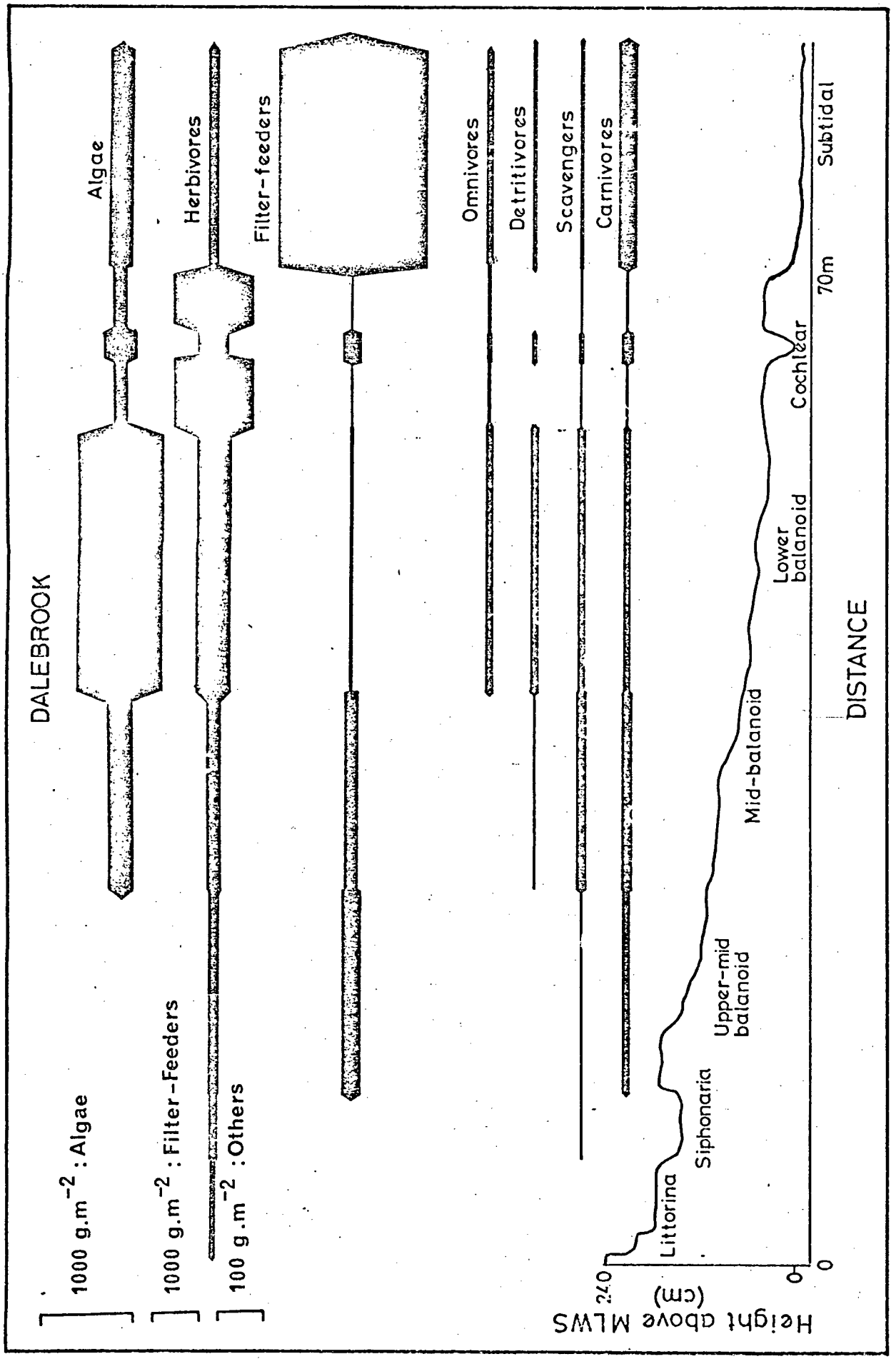


Fig. 1.28 Profile diagram of Dalebrook.

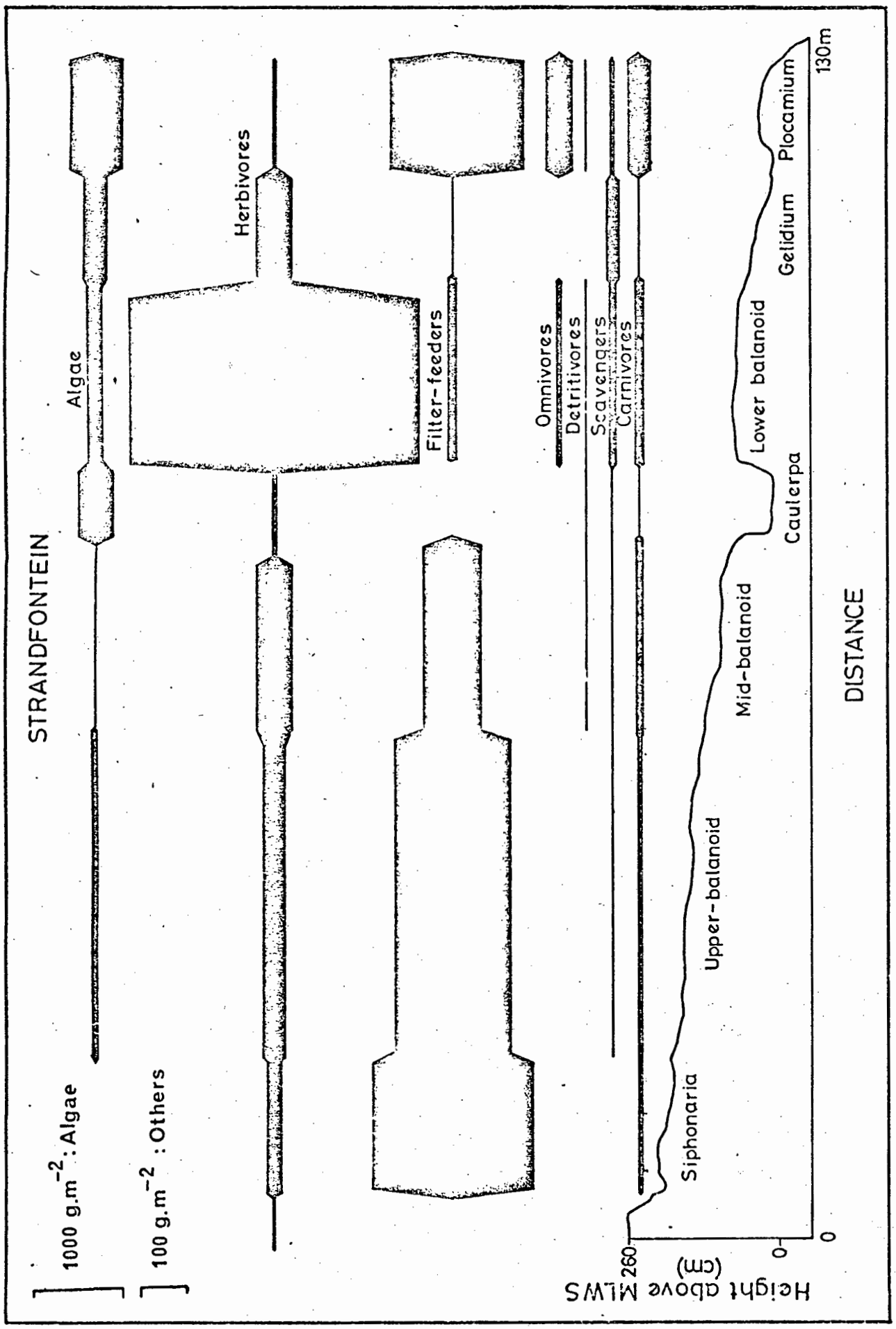


Fig. 1.29 Profile diagram of Strandfontein.

blanketing effect detrimental to the feeding of some filter-feeders. Movement of the fronds when submerged may also be important by preventing or interfering with the settlement of larvae.

In the lower regions biomass is usually highest in the subtidal fringe, if present, or in the lower balanoid zone. These fringes are usually dominated by particular species (especially Bifurcaria brassicaeformis, Champia lumbricalis, Plocamium corralorhiza and P. cornutum) at extremely high densities. The influence of heavy grazing on algal biomass is well documented (eg. Southward, 1969; Branch, 1971; Dayton, 1971). Biomass of algae in the cochlear zone is generally low and algae tend to be denser both above and below this zone on almost all beaches (see figs.1.30-1.32), this is probably due to heavy grazing of spores by Patella cochlear which completely dominates this zone. Although P. cochlear is absent from Strandfontein, P. barbara seems to fulfill a similar ecological role. Algal biomass is again low where P. barbara is abundant.

Lower balanoid algal biomass is almost invariably lower than in the subtidal fringes but may still attain high values and is generally higher than in the cochlear zone (figs. 1.30-1.32). Important lower balanoid species include Ulva spp., Gelidium pristoides, and Gigartina radula. On cold water beaches, Arthrocardia sp. is sometimes abundant in this zone as is Aeodes orbitosa which may form distinct sub-zones (eg. Kommetjie). Neither of these algae is abundant in the lower balanoid of warm beaches although the former is generally abundant in the cochlear zone. Sub-zones of the low balanoid are also formed on some beaches by particularly dense beds of Bifurcariopsis capensis (Buffels Bay A), Champia lumbricalis (Robben Island), Bifurcaria brassicaeformis (Robben Island, Buffels Bay B, Froggy Pond B) and Gelidium pristoides (Strandfontein).

A pattern thus emerges of very high algal biomass in the subtidal fringe, decreasing dramatically in the cochlear zone due to grazing and increasing again in the lower balanoid.

The exceptions to this pattern are Froggy Pond A, Olifantsbos and Kommetjie. Algal biomass on the first two of these does decrease dramatically in the cochlear zone but fails to increase again in the lower

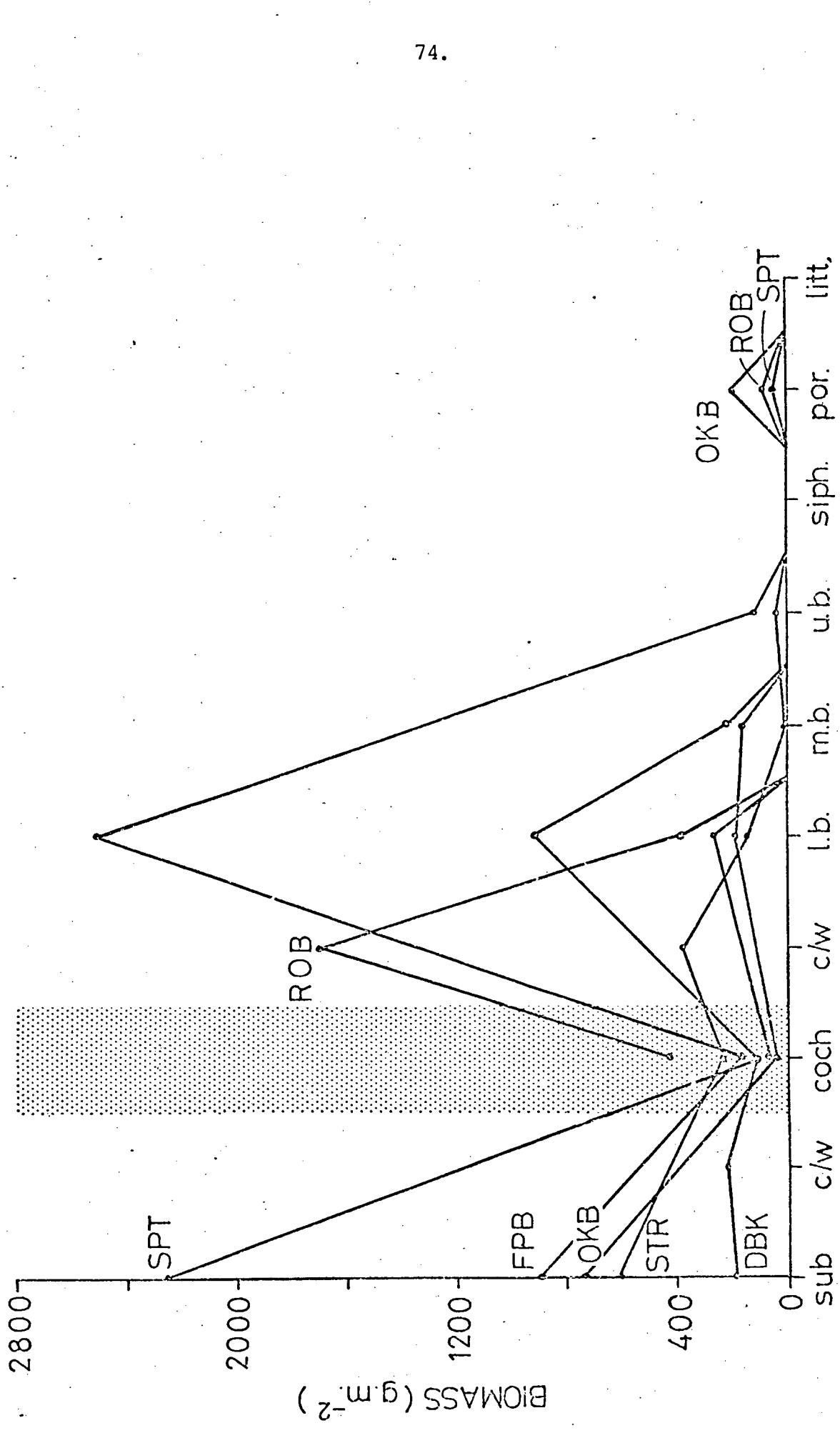


Fig. 1.30 The relationship between zonation and algal biomass on exposed beaches.

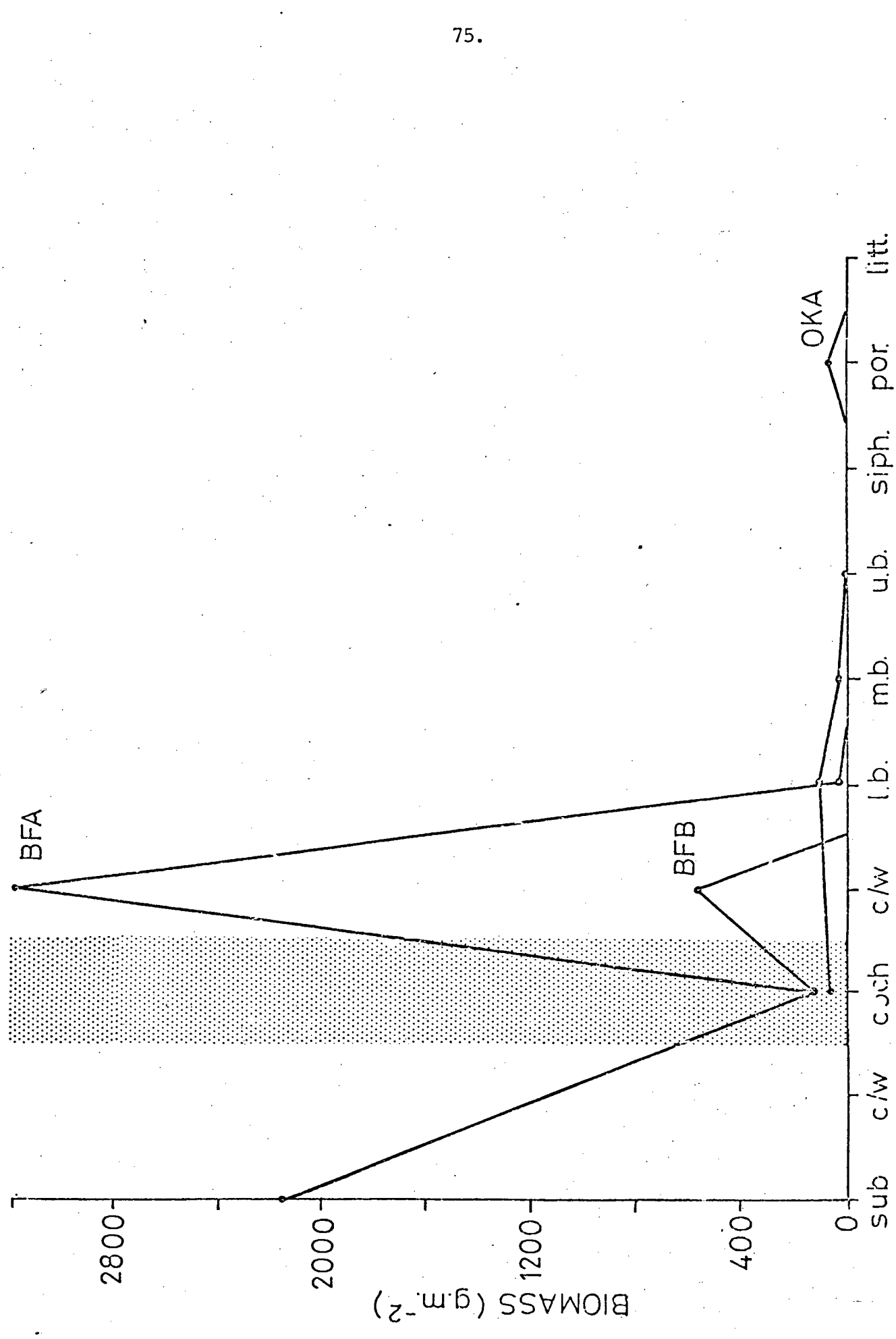


Fig. 1.31 The relationship between zonation and algal biomass on sheltered beaches.

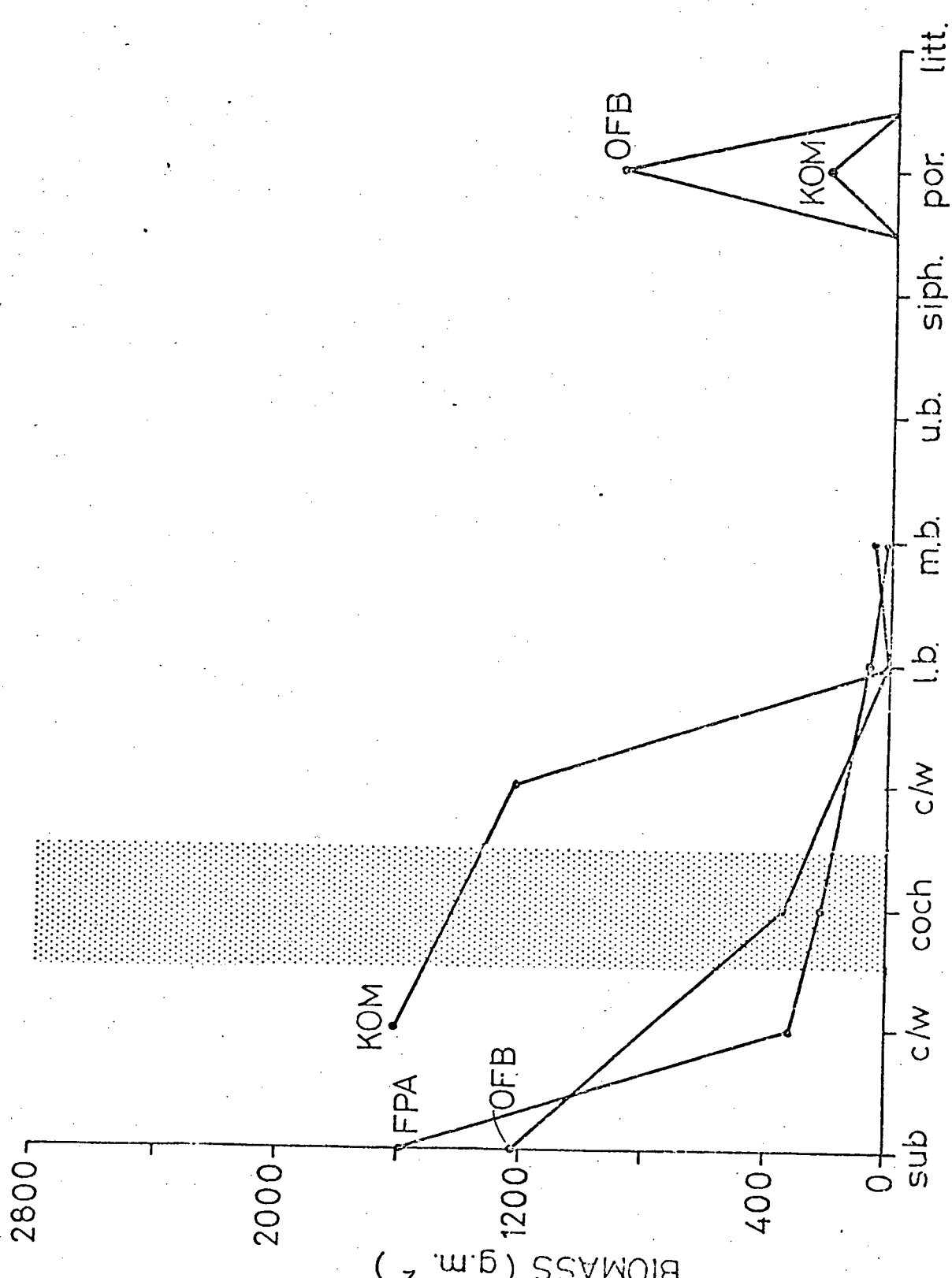


Fig. 1.32 The relationship between zonation and algal biomass on aberrant sheltered beaches.

balanoid. This may be due to a reduction in wave exposure leading to increased desiccation rates as both of these beaches are sheltered. Kommetjie is also sheltered with a reduced biomass in the lower balanoid. P. granatina is particularly abundant in the lower balanoid here and may have a grazing effect similar to that of P. cochlear. Kommetjie is also unusual as the cochlear zone is very poorly developed and overlaps with the subtidal fringe to form a cochlear weed zone. Similarly the cochlear zone at Olifantsbos is scattered and poorly defined. P.cochlear tends to be more abundant on exposed shores (Branch, 1975a) and the unusual condition of the cochlear zone at these two beaches may be due to their sheltered nature.

The effects of P. cochlear on algal biomass and the consequent influence on species richness (p. 18) highlight the importance of this key lower shore species.

2. Herbivores

Although the herbivore compartment contains many species biomass is dominated by the large limpets (see above). Highest biomass occurs in the cochlear zone where P. cochlear may reach extremely high densities. At Strandfontein, where P. cochlear is absent, herbivore biomass is dominated by P. barbara which occupies the equivalent zone. Biomass may also be high in the mid or upper balanoid. High biomass in these zones is usually attributable to a small number of species. P. granularis is abundant in the mid balanoid at Oudekraal B and Strandfontein, in the upper balanoid at Oudekraal A, Froggy Pond B and Seapoint and also in the Porphyra zone at Olifantsbos. The winkles Oxystele variegata and O. tigrina form the bulk of herbivore biomass in the mid balanoid at Buffels Bay B along with P. oculus. O.variegata also reaches high levels of biomass in Porphyra zone and, in conjunction with Helcion pectunculus, in the upper balanoid at Olifantsbos. It also forms the bulk of herbivore biomass in the upper balanoid at Froggy Pond B.

Although Siphonaria spp. are often very numerous on the upper shore they rarely produce a high biomass due to their small size. One exception to this is the Siphonaria zone at Olifantsbos, where Siphonaria spp. density is very high.

Thus high herbivore biomass in different zones may be largely ascribed to limpet and Oxystele distribution, the main zones being:

cochlear zone	-	P. cochlear
mid balanoid	-	P. granularis, sometimes O. variegata and P. oculus.
upper balanoid	-	P. granularis, O. variegata, H. pectunculus.

The lower balanoid is generally dominated by algae and herbivore biomass is usually low.

There are 2 important exceptions to this. At both Kommetjie and Strandfontein algal biomass is unusually low in the lower balanoid and herbivore biomass is high. Again this is due primarily to limpet abundance. At Kommetjie the bulk of low balanoid herbivore biomass (94,09 %) is formed by P. granatina. At Strandfontein P. barbara dominates the lower balanoid including the region which would be occupied by P. cochlear on other beaches. The reasons for this are discussed below (chapter 4).

3. Filter-feeders

As filter-feeder biomass is markedly higher on exposed beaches (Table 1.7) zonational trends are more readily observed by examining these beaches alone. The trends recognised do however apply to sheltered beaches as well.

Examination of the profiles reveals that filter-feeders tend to form low and middle/high shore populations. Low shore populations are dominated by mussels in conjunction with barnacles and on some beaches the tunicate Pyura stolonifera. Mid and upper shore populations are dominated by barnacles. It is interesting that the cochlear and lower balanoid zones generally have reduced biomass of filter-feeders. This is presumably due to grazing of larvae by limpets in the former and the blanketing effect of dense algal populations in the latter.

From Table 1.11 it can be seen that different species tend to dominate on cold and warm beaches. This may be summarized as follows:

TABLE 1.11 : PERCENTAGE COMPOSITION OF FILTER-FEEDER BIOMASS IN ZONES OF HIGH FILTER-FEEDER BIOMASS ON EXPOSED BEACHES

Beach Zone	Aula-comya ater	Choro-mytilus meridi-onalis	Perna perna	Mussel Total	Balanus algi-cola	B.maxi-laris	Octo-meris angu-losa	Tetra-clita ser-rata	Bar-nacle Total	Pyura stolo-nifera	Overall Total	Filter-feeder biomass ($g.m^{-2}$)
SPT cochlear	43,23			43,23			56,77		56,77		100,00	266
L.balanoid	91,23	7,02		98,25			0				98,25	57
U.balanoid				0			21,05	78,98	100,00		100,00	19
OKB Subtidal	99,30			99,30		0,7			0,7		100,00	1283
M.balanoid	14,51			14,51			85,49		85,49		100,00	689
U.balanoid gulley	1,73			1,73				98,27	98,27		100,00	405
ROB cochlear	59,69			59,69			40,31		40,31		100,00	191
Bifurcaria	50,15			50,15			49,26		49,26		99,41	339
Champia	100,00			100,00					0		100,00	338
L.balanoid	1,33			1,33			96,22	0,82	97,04		98,37	978
M.balanoid				0				100,00	100,00		100,00	155
FPB Subtidal	33,89		17,78	51,67	6,69		3,77		10,46	36,40	98,53	478
L.balanoid	28,26	1,45	11,59	41,30	56,52				56,52		97,82	138
U.balanoid	1,07			1,07			98,79	0,14	98,93		100,00	6600
DBK Subtidal	0,11			0,11		0,19	16,60		16,79	83,09	100,00	3614
Hypnea	0,53		2,67	3,20			56,80		56,80	37,87	97,87	375
M.balanoid				0			0,90	98,65	99,55		99,55	222
U.balanoid				0				100,00	100,00		100,00	317
STR Subtidal	3,75		39,25	43,00					0	57,00	100,00	293
L.balanoid	39,62		51,15	90,77					0		90,77	26
M.balanoid				0				99,42	99,42		99,42	173
U.balanoid				0				100,00	100,00		100,00	267
Siphonaria				0				100,00	100,00		100,00	377

(i) Cold beaches : low zones (subtidal fringe, cochlear and sometimes lower balanoid) are dominated by Octomeris angulosa and Aulacomya ater. Upper zones (mid and upper balanoid) are dominated by Tetraclita serrata. At Seapoint (SPT) upper shore filter-feeder biomass is low and T.serrata is joined here by O. angulosus.

(ii) Warm beaches : low zones at Froggy Pond and Strandfontein are dominated by Pyura stolonifera in conjunction with the two mussels A. ater and Perna perna. At Dalebrook mussels are less important and O. angulosa is abundant in the subtidal fringe. The middle and upper zones are again dominated by T. serrata at Dalebrook and Strandfontein and by O. angulosa at Froggy Pond B.

Thus we can see that low zone populations are composed primarily of A. ater along with O. angulosa on cold beaches and with P. stolonifera and P. perna on warm beaches. The single exception to this is Dalebrook where mussels are not abundant. The upper zones on all beaches are dominated by the barnacle T. serrata which is joined by O. angulosa at Seapoint. O. angulosa replaces T. serrata in the upper balanoid at Froggy Pond B where it forms 98,79 % of filter-feeder biomass. O. angulosa is a particularly interesting species as it is found only on exposed shores and is thus a good indicator of exposed conditions. The unusually dense population of O. angulosa at Froggy Pond B may be indicative of particularly exposed conditions.

4. Carnivores

Highest carnivore biomass generally occurs in zones where filter-feeder biomass is high, although not all dense filter-feeder populations are associated with high carnivore populations (fig. 1.33). Carnivore biomass consists largely of errant polychaets and gastropods. Only the latter (eg. Thais spp.) are capable of preying on mature barnacles or mussels.

It seems likely however that the polychaets may feed on smaller species sheltering among the filter-feeders (increased biomass of many of the smaller species where filter-feeder biomass is high has been mentioned), and perhaps on very small juveniles of the filter-feeders themselves. For example very small mussels have been found in the gut of errant polychaets (pers. obs.).

Carnivore biomass thus follows a similar pattern to that of filter-feeders and is higher on exposed beaches. Although a direct relationship between biomass of filter-feeders and carnivores is not implied an indirect relationship may exist. Thus the coefficient of determination between filter-feeder and carnivore biomass is low ($r = 0,70$) but a trend is still apparent.

5. Omnivores

Omnivore populations are primarily low shore, the bulk of biomass being composed of Pseudonereis variegata as described above. P. variegata is most common among algal tufts or beds of filter-feeders. Some mid or upper shore populations of omnivores do occur however:

1. At Olifantsbos the holothurian Cucumaria frauenfeldii occurs in the mid balanoid forming a small omnivore population.
2. At Froggy Pond B the lower balanoid population is formed by P. variegata and the holothurian Thyone aurea among the dense weed beds while the larger upper shore population is due to the abundance of P.variegata among the dense Octomeris beds.

6. Detritivores

Low shore populations of detritivores occur on both warm and cold shores and are largely associated with algal beds. These populations

vary in composition according to their zonation. Parechinus angulosus generally accounts for the bulk of detritivore biomass at Seapoint and on warm beaches, as described, and is usually found only in the lowest zones or in pools and gulleys. The remaining detritivore species tend to be zoned as follows:

In the subtidal fringe sedentary polychaets are important. Among these the most abundant are Cirriformia capensis, C. sp. and Orbinia sp. Cochlear zone populations are largely composed of ophiuroids such as Amphipolus integer and Amphipholis squamata. These also occur in the lower balanoid populations along with C. capensis. Various amphipod and isopod species (eg. Janiropsis palpalis and Stenetrium sp. (Isopoda) and Amaryllis macropthalma and Ischyrocerus anguipes (Amphipoda) occur among the algae of both the low balanoid and the subtidal fringe.

On warm beaches upper balanoid populations of detritivores also occur and include the sedentary polychaets Pherusa laevis (upper balanoid) and Orbinia angrapequensis (in some upper balanoid pools).

Thus there are low shore populations on both warm and cold beaches consisting of P. angulosis or polychaets and ophuiroids along with some amphipods and isopods. Upper balanoid populations composed of polychaets, occur on some warm beaches.

7. Scavengers

Scavenger populations are composed largely of isopod species, a few amphipods and the whelks Burnupena spp. Crustaceans are common among algae where some species may be very abundant, particularly the amphipod Paramoera capensis and the isopods Dynamenella huttoni, Exosphaeroma laeviusculum and E. varicolor. Burnupena is generally common below mid tide and the most common species is B. delalandii, which also preys on living winkles (see Chap. 7). Scavenger populations occur in almost all zones. There is no obvious zonational effect on scavenger biomass beyond a decrease with increasing height and a slight tendency for biomass to be higher where algae or filter-feeders offer a more favourable micro-habitat.

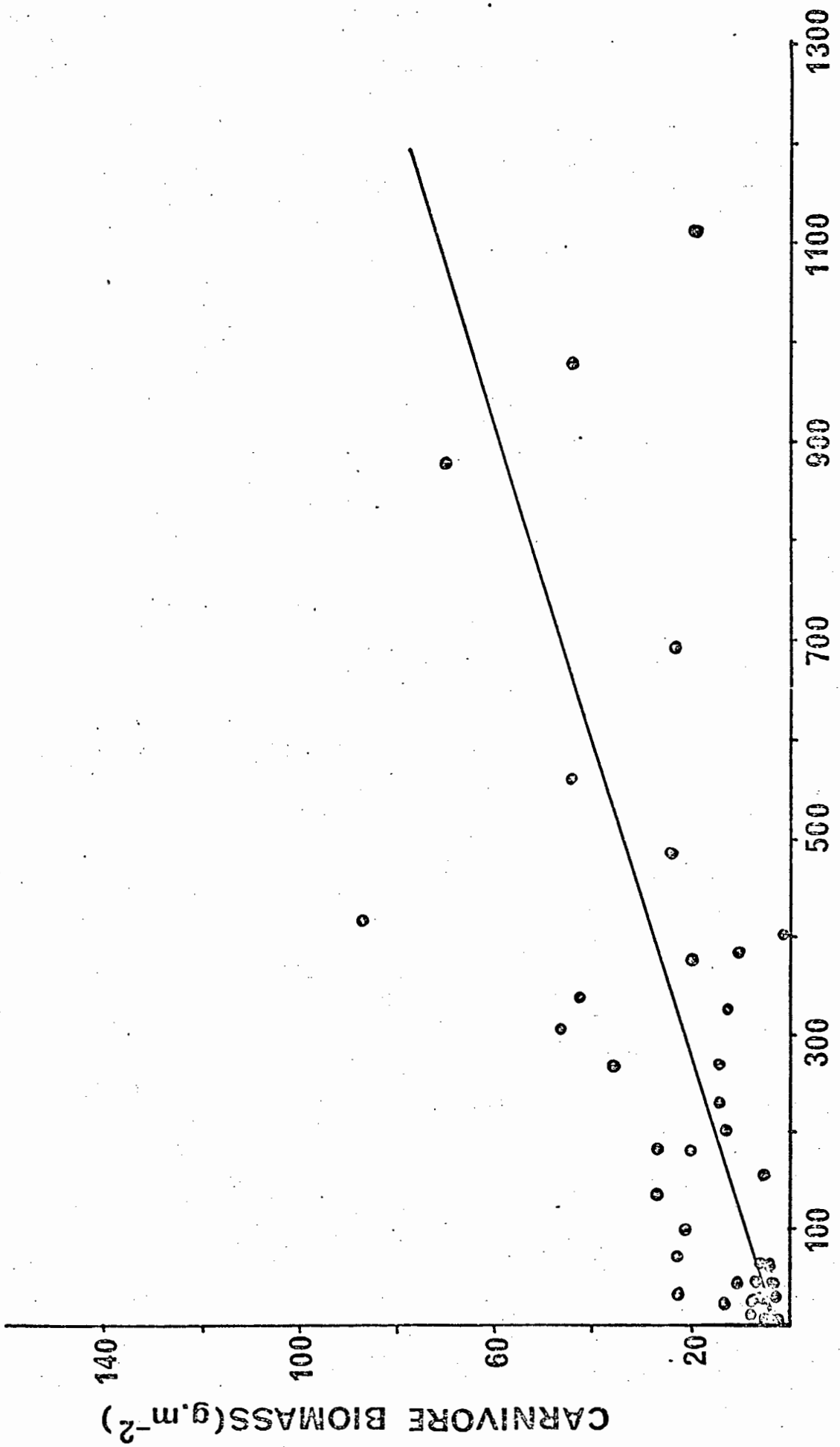


Fig. 1.33 The relationship between filter-feeder biomass and carnivore biomass (y=4,37+0,06x;r=0,70)

SUMMARY

1. Zonation patterns for 12 beaches on the Cape Peninsula, South Africa, are described and the diversity of beach types and the extreme heterogeneity of each beach is emphasised.

2. Two boulder beaches were considered (Oudekraal A and Buffels Bay B). The substrate on these is unstable and results in a particularly low mean biomass and species richness.

3. Total biomass was found to be higher for exposed beaches and different patterns of trophic dominance prevail on exposed and sheltered beaches. Biomass is dominated by algae on sheltered beaches. Filter-feeders, carnivores and omnivores all have a higher biomass on exposed beaches. Filter-feeders are particularly important and dominate biomass on most exposed shores. Carnivore biomass is thought to be indirectly related to the biomass of filter-feeders.

Omnivore biomass and detritivore biomass are dominated by Pseudonereis variegata and Parechinus angulosus respectively. Trends of biomass for these two compartments therefore merely reflect trends in the biomass of these two species.

Herbivore biomass was found to be higher on broad, flat beaches than on very steep shores. Patella spp. constitute a significantly higher proportion of herbivore biomass on the former.

Two basic types of beaches can therefore be distinguished: exposed and sheltered. Differential trophic dominance probably leads to fundamentally different patterns of energy flow on these two types.

4. Strong zonational trends were found in both species richness and the biomass of the most important trophic compartments. Richness declines farther up the shore. Herbivore and algal biomass are also highest at the bottom of the shore. Algal biomass declines sharply in the cochlear zone, probably because of grazing effects. This leads to a decrease in species richness in this zone. On exposed beaches filter-feeder biomass is high in the subtidal fringe where mussels, particularly Aulacomya ater, and on warm beaches, Pyura stolonifera are important. Filter-feeder biomass is also high on the upper shore where barnacles, particularly Tetraclita serrata, predominate.

5. Certain species emerge as being of particular importance to energy flow through these intertidal communities. These include Aulacomya ater, Tetraclita serrata, Patella cochlear, P. granatina, P. granularis, Oxystele variegata and the algae Bifurcaria brassicaeformis, Gelidium pristoides, Ulva spp. and Gigartina radula.

Reduction of both algal biomass and species richness in the cochlear zone indicate the importance of P. cochlear as a key species in structuring the communities of the lower shore.

CHAPTER 4 : SIMILARITY ANALYSIS OF BEACH TYPES

INTRODUCTION

Examination of trophic compartments yields some understanding of the major trends of community structure in response to the three physical factors under consideration. By summing species data into trophic data, however, a considerable amount of information is lost. Trophic data does not include information on differences in species composition.

Different beach types may be related in the nature of their trophic structure. But they may reveal completely different relationships when species composition is considered instead. This again raises the problem of the vast complexity of these communities. It is possible to consider distributional patterns of the major species. It is however very difficult to include information on the many minor species which all contribute, in less obvious ways, to the complexity of biotic interactions and micro-environment. For example, two beaches may support beds of a particular algal species and yet the epifauna and associated smaller algae may be completely different. While the more abundant species have a dominating biotic effect these smaller species may each have significant influences. Biotic richness is due largely to these smaller species and differences in their composition may be important.

It is necessary to consider all species if we are to maximize information usage in examining beach communities. This problem is compounded by the fact that not only species presence but also the abundance of each species is important.

A data matrix on the scale of the one generated in the present study may only be fully utilised with the aid of mathematical analysis. Indeed this analysis itself is extremely cumbersome without the use of a computer system.

In order to compare beach biota under different conditions in terms of the abundance of all species recorded the data were examined

using a computerised similarity analysis. The choice of analysis strategy is itself important and will be considered below.

Further aspects of these communities were investigated by deriving (a) Species richness, diversity and evenness; and

(b) Indicator species for different physical conditions.

Much attention has been paid in the past to the effects of various physical factors on rocky intertidal species and communities. In particular, work has been carried out on isolating and examining the effects of temperature, wave exposure and substrate. This section is an examination of the inter-actions of these three factors in influencing rocky intertidal communities (ie. the assemblages of species occupying rocky shores) in the Cape Peninsula.

Temperature

Temperature has long been recognised as a major factor governing species distribution (eg. Isaac, 1938; Stephenson, 1944; Crisp and Southward 1958; Lewis, 1965). Some possible mechanisms for temperature-based control of distribution have been examined by, for example, Orton (1920), Hutchinson (1947), Southward and Crisp (1956), Crisp (1957), Southward (1955, 1958a), Lewis (1964).

Within a given temperature regime the type of substrate and degree of wave exposure may have important modifying effects on the communities present.

Substrate

Stability of substrate is obviously important, boulder beaches may subject the species present to rolling and crushing effects during rough weather. Given a stable substrate, the type of rock is important in terms of weathering and settlement of sedentary forms. Suitability for colonization may depend on species preference (Moore and Kitching, 1939), either due to different larval responses (eg. Barnes and Powell, 1950) or sub-optimal conditions for adults. Larval responses may be influenced by substrate hardness (Southward and Crisp, 1954; Stephenson, 1961; Stephenson and Searles, 1960) and smoothness (Crisp and Barnes, 1954; Hatton, 1938, quoted in Moore and Kitching, 1939; Barnes and Powell, 1950). Angle, colour and light reflecting properties of the substrate may also be important (Pomerat and Reimer, 1942; Williams G.B., 1964). Adult forms may be affected by desiccation on very porous rocks (Moore and Kitching, 1939) or interference with locomotion on very rough surfaces (Southward and Orton 1954). Harlin and Lindbergh (1977)

observed no significant differences in settlement of algal spores on substrates of varying particle size. They did however find that with time, significant differences in population developed due to the different particle size preference of the species examined. In addition to these direct effects substrate affects beach morphology (due to characteristic weathering of different rock types) and may thus influence exposure. Very steep shores tend to experience more violent wave action etc.(Lewis, 1964). Conditions on adjacent areas may also be important. For example, nearby sandy beaches may lead to a sand scouring effect on rocky shores (eg. Daly and Mathieson, 1977).

Exposure

The degree of wave exposure has effects operating at two levels, wetting and damage (Southward, 1958b). Increased exposure results in a larger spray zone and an upward extension of vertical distribution for most species. Waves are important in supplying nutrients, removing wastes, mixing of gases etc. However excessive exposure leads to physical damage or removal of species. Consequently areas with a strong tidal flow but no violent wave action support very rich and diverse communities as they experience the advantages of good water exchange without the disadvantages of wave damage (Lewis, 1968). Species have different exposure preferences and there are species which are positively, negatively or not correlated with increased exposure. Filter-feeders such as barnacles and mussels usually increase in size with increased exposure (Moore, 1935; Southward and Orton, 1954; Jones and Demetropoulos, 1968). The size and density of molluscs has also been correlated with the degree of exposure (Meyer and O'Gower, 1963; Crapp, 1973; Branch, 1975a; Heller, 1976).

Wave exposure, in combination with dessication effects has a major influence on algal distribution patterns (Dayton, 1971). Grubb (1936) showed that each dominant algal species has a definite optimum range of exposure beyond which it does not flourish. Kingsbury (1962) found an increase in the number of species of algae in Massachussets with increased exposure although the total biomass remained roughly constant. In contrast to this, Southward and Orton (1954) found that algal distribution and abundance at Plymouth decreased with greater

exposure and Hallfors et al (1975), working in the Baltic sea, found that biomass of both plants and animals was lower in very exposed rather than moderately exposed sites. These discrepancies may be due to different tolerances of the species examined (the sites being geographically widely separated) or the analyses may have been based on different degrees of exposure. Although various effects of exposure are widely recognised, quantification of the degree of exposure is a matter of some difficulty. Exposure may be measured in physical terms (eg. the turbulometer designed by Field, 1968, plaster of Paris "clod cards" used by Doty (1971a) or measurement of drag by Jones and Demetropoulos, 1968) or it may be scaled according to a biological scale (eg. Ballantine, 1961; Taylor, 1971). For biological exposure scales, exposure is considered as a trend in the composition of the shore flora and fauna. The abundance of common species on well known shores is used to produce a comparative scale of exposure for other beaches in the same region (Ballantine, 1961). Physical measurements should be taken over a period of at least a year while there are, so far, biological scales for only a few very local areas. Most work is of a comparative nature where beach A is considered to be more exposed than beach B etc. In the absence of physical measures beaches can usually be ranked according to exposure on a subjective basis. Although subjective, such assessments are generally accurate within the local context, and can lead to meaningful results.

Conditions of exposure, substrate and temperature in the study area have been described above (p.7).

METHODS

Biomass data were collected for all recognisable zones and subzones on each beach as described above (p.10). Species biomass in different zones on the same beach generally varies considerably. In order to compare beaches with each other a measure of biomass of each species on the entire beach is required. Extrapolation of biomass from each zone to the whole beach on the basis of the area of each zone brings in the problem of the size of each beach. Extrapolation was therefore carried out by considering the proportion that each zone formed of the whole beach.

The maps produced for each beach (figs. 1.5 - 1.15) give an accurate measure of the areas occupied by each zone, which were derived as a percentage of the total beach area for every zone, using a combination of stereoscopic matched pairs of aerial photographs and local topographic surveys. The photographs were kindly taken by Mr. H. Rüther of the Department of Land Survey, U.C.T. and were taken at an average height of 1000 feet (scale 1:2000).

The percentage of each zone was used as a weighting factor for biomass values using a simple computer programme. Biomass for every species in each zone was multiplied by this factor and divided by 100 (as the percentage is a fraction) to give a mean biomass for the whole beach.

eg. Consider species x which has a mean biomass of 300 g/m^2 in zone y. Zone y constitutes one third of the total beach area. The mean biomass of x for the whole beach is then derived as :-

$$\frac{\text{biomass x percent}}{100} = \frac{300 \times 33{,}33}{100} = 100\ g/m^2$$

Total mean biomass of each species was then obtained by summing the mean biomass derived from each zone. In this way the data matrix of 113 zones versus 310 species was reduced to one of 12 beaches versus 310 species which was then used in the similarity analysis.

ANALYSES

Cluster-analysis

The raw data matrix contained biomass values for 310 species at 12 beaches. Due to the absence of species from many beaches the matrix contained a high proportion of zero values. Analysis was done by means of classification. This is a method of deciding whether individuals (ie. beaches) may validly be grouped into sets and if so to delineate these sets (Kendal, 1966). Classification involves the erection of a similarity matrix based on a measure of similarity between samples and a clustering of the samples into sets on the basis of the similarity matrix.

The similarity measure used was the Czekanowski coefficient, defined by Bray and Curtis (1957) as

$$C = \frac{2w}{a+b}$$

a = sum of quantitative measures of all species in one sample
b = sum of quantitative measures of all species in second sample
w = sum of lesser values for those species common to both samples.
Thus if both samples have identical scores for all species C = 1.

This is a coefficient of association which excludes double-zero matches. Inclusion of double-zero matches implies that two samples are similar if they both lack certain species. In a very homogenous system this may be valid, however in a heterogenous system it can lead to nonsensical conclusions. The Czenkanowski coefficient is based on quantitative rather than presence/absence scores. This is more efficient in data utilisation and is more realistic ecologically. Biomass values were converted to log biomass values before analysis following Field (1971) and Field and MacFarlane (1966), as this prevents swamping of the data by very high values (Field, pers. com.1979).

The main clustering methods have been reviewed by Williams (1971). The choice of method is important as the intensity of clustering of the data is as much a property of the analytic method used as of the data itself. The polythetic "group average" technique was

chosen. Polythetic techniques examine all attributes of each sample unlike monothetic methods which use single attributes as dichotomous dividing points between groups. The groups average strategy joins two samples at an average level between the two groups and is intermediate in its clustering intensity between the Nearest Neighbour and the Furthest Neighbour techniques. The chief advantage of such a space conserving strategy is that it does not impose enhanced clustering which may lead to misclassification of the data. In addition the problem of the group-size dependence of space dilating strategies does not arise (Stephenson et al, 1972). Although some information loss or distortion has been shown for this strategy (Hall, 1969a) this is usually minimal (Hall, 1969b) and it has been successfully used by Field (1970, 1971) and Campbell and Moll (1976).

Analyses were performed on the full data matrix using the Group Average, Furthest Neighbour and Nearest Neighbour strategies yielding results in the form of dendrograms. Interpretation is difficult when three variables are involved. To clarify the importance of particular variables, separate analyses were performed on selected groups of beaches with one variable in common and on all beaches using data on single trophic compartments only.

Multi-dimensional scaling (MDSCAL)

Use of dendrograms gives an easily understandable interpretation of data. However, the disadvantage of representing the information in a large data matrix by a dendrogram classification lies in the distortion inherent in fitting a one-dimensional model to the data. This may be overcome by application of a multi-dimensional scaling technique (MDSCAL) which may be based on the same matrix of similarity values as the cluster analysis. Multi-dimensional scaling is a means of deriving n points whose interpoint distances geometrically represent the experimental dissimilarities of n objects (Kruskal, 1964). In this study the points represent beaches. The interpoint distances equate to overall ecological differences between beaches as revealed by variations in species biomass.

These points may be plotted to give a geometric configuration in one or more dimensions. In doing so we again impose a degree of distortion on the data which decreases as more and more dimensions are considered. Consideration of 310 dimensions in this case would result in zero distortion as variation according to all attributes (ie. 310 species) could be represented. This of course negates the basic purpose of analysis, which is to render the data into a more comprehensible form. A compromise is possible by measuring the distortion or "stress" imposed on the data by considering any particular number of dimensions. Stress is a measure of how well the 1,2 or multi-dimensional configuration derived fits the data. The stress value may be compared with a scale where percentage of stress is equated to a goodness of fit evaluation ranging from "poor" to "perfect" (eg. Kruskal, 1964; Kruskal and Carmone 1969). Application of these labels must be guarded (Arabie, 1978) but the basic worth of the algorithm still stands.

The similarity matrix derived by the Czekanowski coefficient was subjected to a multi-dimensional scaling analysis using a computer programme written by Kruskal. In this analysis 1-6 dimensions were considered. Although MDSCAL with more than 2 dimensions allows a less distorted representation of data than cluster analysis, it gives no indication of percentage similarities between groups. Also, the results, with more than 3 dimensions, are difficult to represent or interpret visually. General consideration of the data is therefore based on dendrogram analyses. MDSCAL analysis is used to derive an idea of the distortion involved in data presentation and also to give a better insight into the true configuration of dendrogram results.

Information statistic and U-tests

Indicator species characterising water temperature, wave action and substrate type were derived using the information statistic for hypothesis testing or I-test. Each attribute of a pair of samples makes a contribution to the total information difference between the

samples. If this contribution is large enough the attribute may be used as an indicator attribute for one of the sets at a known level of confidence (Lambert and Williams, 1966; cited in Field, 1969). The confidence limit used was 95% and I-tests were carried out on presence/absence data. Significant differences in biomass of each species in different sets of beaches were examined using the non-parametric Mann-Whitney U-test. The members (or species) of both sets are listed together in order of descending biomass and each member is assigned a rank value according to this list. U is then calculated as :

$$U = n_1 n_2 + \frac{n_1 (n_1 + 1)}{2} - R_1$$

(Siegel, 1956)

where n_1 and n_2 give the size of the two samples or sets of stations and R_1 is the sum of the ranks assigned to sample 1. Again the 95% confidence limit was used. Biomass varies considerably between different zones on the same beach. In order to compare biomass between beaches, mean biomass values for each entire beach were used rather than mean biomass within the specific zones only. This has the disadvantage of using a derived value rather than a measured value. It does however give a more realistic assessment of biomass for the whole beach as the zones occupied by any one species may form only a small proportion of total beach area.

A species may show significant differences in either or both of these analyses. Thus three possible contingencies arise:

1) +ve in presence/absence test; -ve in U-test. Such species may occur as only 1 or 2 specimens at each beach in one set but not the other. Species occurring in very low numbers are susceptible to sampling errors and are thus poor indicator species.

2. +ve in U-test but -ve in presence/absence test. Such results, indicate that although the species occurs in both sets it is significantly more abundant in one. It thus indicates trends in abundance rather than acting as a true indicator species.

3. +ve in both tests. Such species may be regarded as good indicator species as they occur in a significant majority of the stations of one group at significantly higher biomass.

Diversity

Diversity of a community has two aspects: species richness and species evenness. Richness (ie. the "areal richness" of Hurlbert, 1971), gives the number of species present but no indication of their relative abundance (ie. evenness of the community). Evenness was obtained using the Shannon-Weaver index of diversity for each beach. This is defined by Pielou (1969) as :-

$$H = -C \sum_j P_j \log P_j$$

where P_j is the probability of a randomly chosen individual from the sample being species j. . In this case P_j is the probability of lg. of dry material from the beach being formed by species j ie. P_j is the proportion of the total biomass constituted by species j. The log base e was used and C taken to be 1 following Pielou (1966).

Evenness indicates whether all species are equally represented or only a few species dominate in terms of biomass. It is derived as :-

$$J = \frac{H}{\log s}$$ (Pielou, 1969)

where H is the diversity of the sample (or community) and s is total number of species present (or richness).

Hurlbert (1971) has pointed out the theoretical failings of diversity indices such as H and contests their "hard" usefulness. They do however give an effective indication of community diversity. H may be influenced by certain properties of the data itself and can only be used for data on a common taxonomic level such as the species (Hughes, 1978).

RESULTS

1. Cluster analysis

(a) Analysis based on data for all species.

In the first analysis temperature was removed as a variable by considering only cold beaches and then only warm beaches.

Cold beaches divide clearly into two sets composed of three exposed and three sheltered beaches respectively (fig. 1.34a), corresponding exactly with the exposure ratings. In the warm beach analysis two sheltered beaches are separated. The sheltered beach FPA however is linked with the exposed beaches (fig. 1.34b). In neither of these analyses is any pattern shown according to substrate.

The significance of substrate and temperature were next examined by performing cluster analyses on (i) exposed or sheltered beaches only and (ii) igneous or sedimentary beaches only.

(i) Sheltered beaches separate into a set of cold and a set of warm beaches (fig. 1.35b) showing no pattern according to substrate. For exposed beaches the pattern is similar though less clear due to the inclusion of the warm beach FPB with the cold beaches (fig. 1.35a). Again no pattern is revealed if substrate is considered.

These analyses, in conjunction with the warm/cold analyses indicate that although substrate may have autecological effects or even important effects on whole groups of species (eg. filter-feeders at Strandfontein, see below) its influence on the community as a whole is masked by the effects of temperature and exposure.

(ii) Interactions of the latter two factors are partially revealed by the igneous/sedimentary analysis. Grouping of igneous beaches (fig. 1.36a) shows the two exposed beaches OKB and FPB to be linked. The two sheltered beaches FPA and OKA are not linked and FPA is associated with the exposed beaches. Initial grouping is however on the basis of exposure. The sedimentary beaches appear to be divided initially on the basis of exposure, so that the sheltered beaches KOM and OFB are linked, and secondly, according to temperature. The two cold

Fig. 1.34-1.42 Results of dendrogram analyses on biomass data, carried out using the Group-Average analysis except where stated.

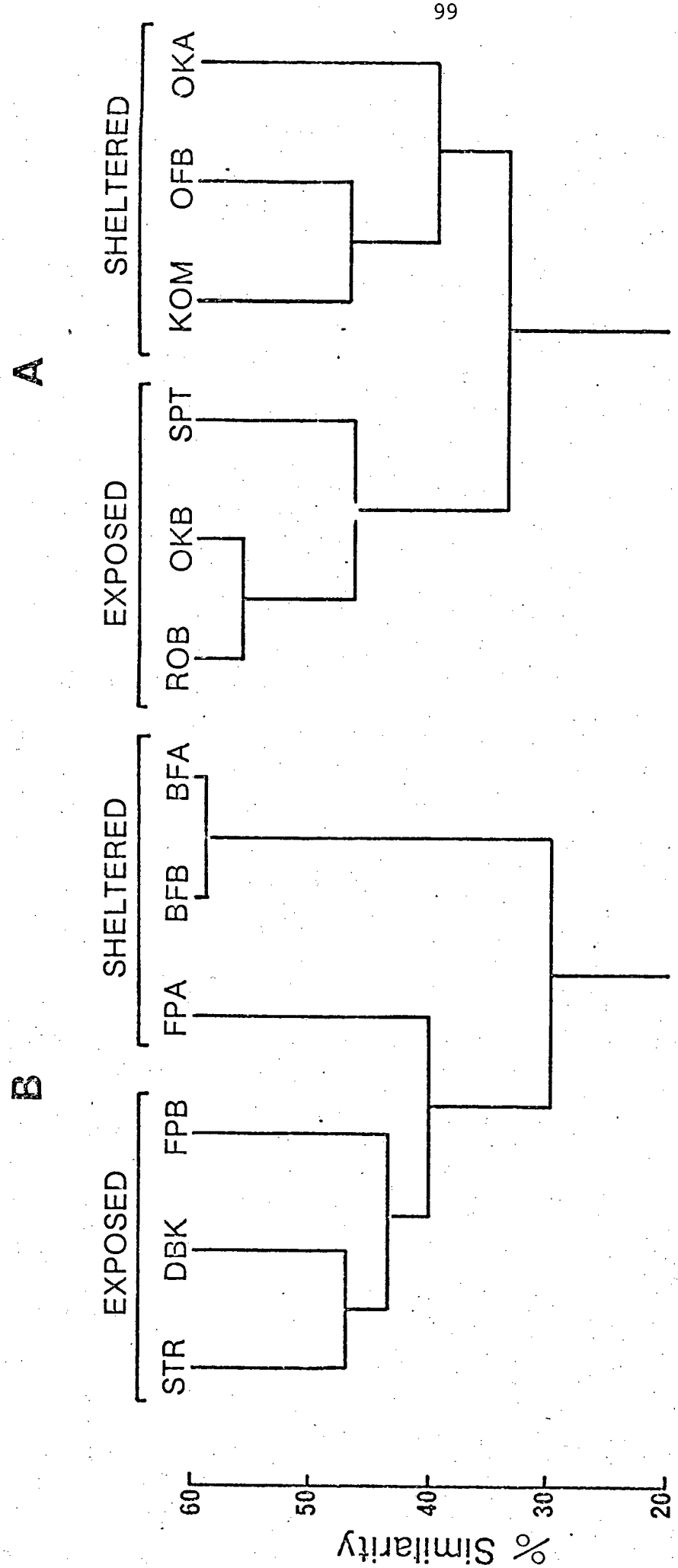


Fig. 1.34 Dendrogram based on data for : A Cold beaches only
B Warm beaches only

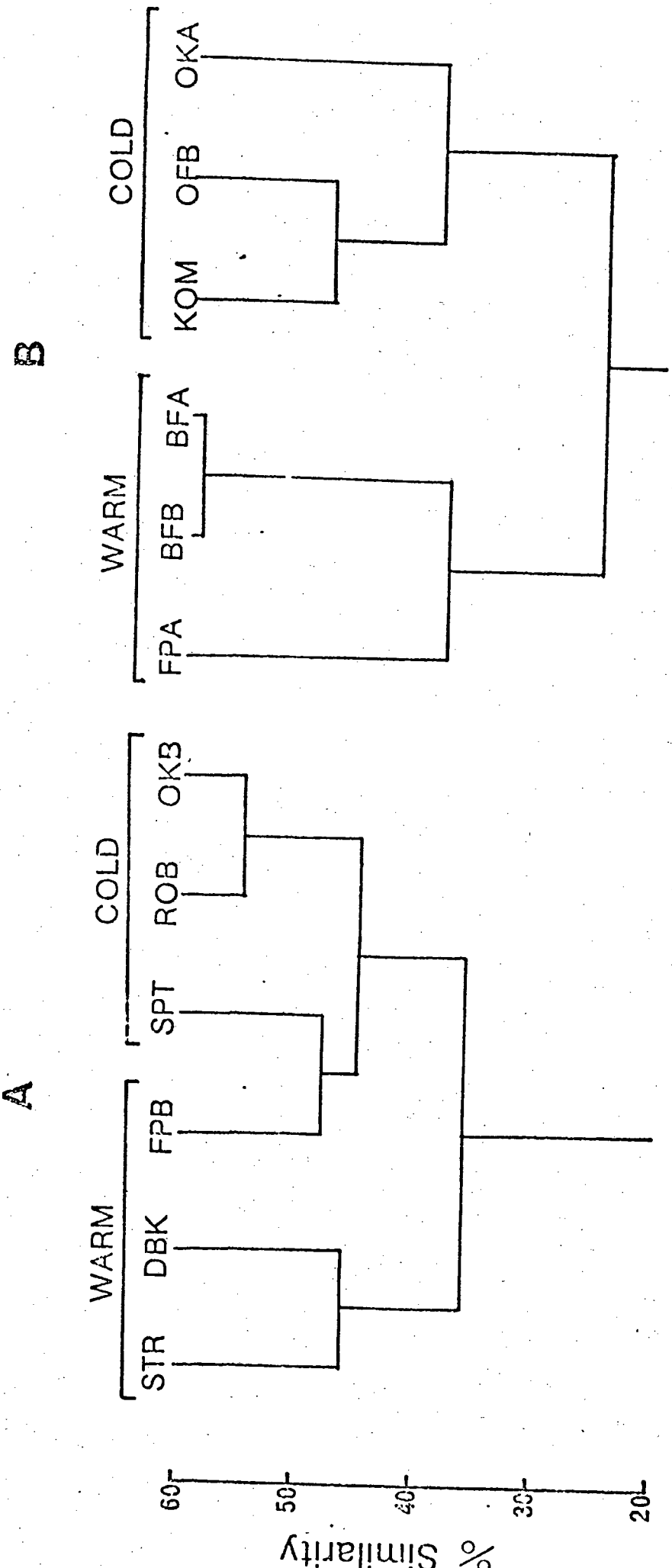


Fig. 1.35 Dendrogram based on data for : A Exposed beaches only
B Sheltered beaches only

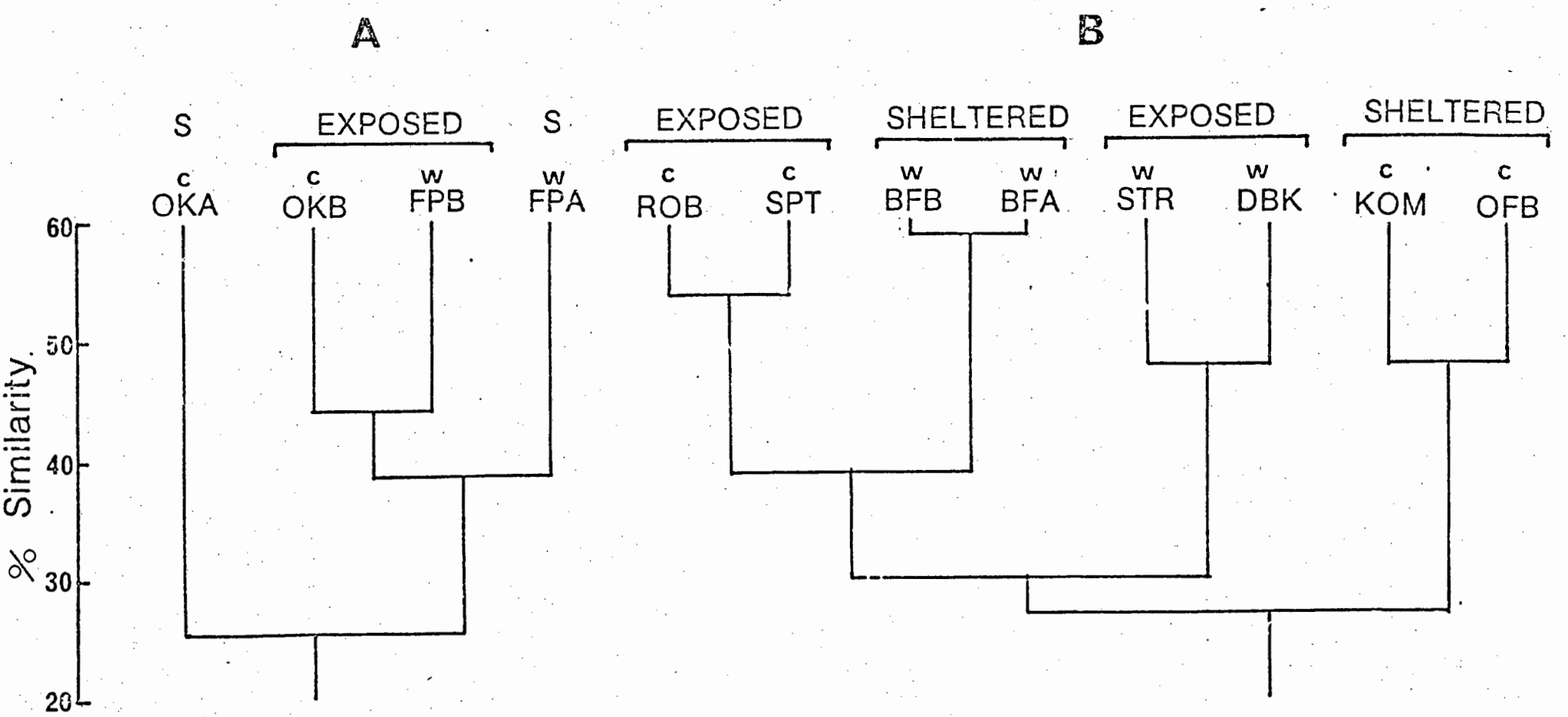


Fig. 1.36 Dendrogram based on data for : A Igneous beaches only
B Sedimentary beaches only

(w = warm, c = cold).

exposed beaches ROB and SPT are grouped separately from the two warm, exposed beaches STR and DBK (fig. 1.36b). This pattern is however confused by the warm, sheltered BFA/BFB pair which are associated with the exposed ROB/SPT pair.

A full analysis for all twelve beaches reveals more clearly the interaction of physical factors.

Analyses according to group-average and furthest-neighbour techniques give identical groupings at different levels of similarity (figs. 1.37, 1.38a). Nearest-neighbour analysis gives almost the same groups fused in a different sequence (fig. 1.38b). This sequence makes less ecological sense overall so that the theoretical grounds for using a group-average strategy are borne out in this case.

The group-average dendrogram (fig. 1.37) shows three main sets:-

1) Exposed beaches (both warm and cold) plus FPA.
2) The paired Buffels Bay beaches.
3) Cold, sheltered beaches.

These sets show no pattern according to substrate. Set 1 shows an example of the group-average effect on data. From the similarity matrix (Table 1.12) it can be seen that SPT is most similar to ROB. ROB and OKB however have a higher similarity and SPT has a reduced affinity for the fused ROB/OKB pair. The reason for the inclusion of FPA in this group is unclear. Omission of FPA from the analysis leaves the pattern identical. Within this set beaches are grouped according to temperature, except for the anomolous FPA/SPT grouping.

Set 2. BFB is unusual (being a very sheltered boulder beach) and if BFA is omitted from the analysis BFB is completely isolated (fig. 1.39).

BFA has its closest affinities with BFB (Table 1.12) and the fused pair is isolated due to the group-average effect as a separate set of warm, sheltered beaches.

We can see then that the beaches are separated according to

TABLE 1.12 : MATRIX OF PERCENTAGE SIMILARITY BETWEEN BEACHES, DERIVED USING THE CZEKANOWSKI COEFFICIENT

	SPT	OKA	OKB	ROB	OFB	KOM	BFA	BFB	FPA	FPB	DBK
OKA	26,779										
OKB	39,218	30,042									
ROB	54,042	30,122	55,853								
OFB	34,460	45,262	42,561	40,413							
KOM	29,184	33,772	38,885	29,649	47,000						
BFA	48,738	24,464	29,708	43,112	28,232	24,268					
BFB	37.750	17,642	19,333	27,358	17,789	13,608	59,171				
FPA	53,600	27,980	33,097	41,426	38,062	32,452	42,340	34,165			
FPB	47,898	15,317	41,440	44,705	22,726	21,873	35,266	19,463	42,492		
DBK	43,114	21,000	42,632	38,759	28,208	33,571	32,460	28,061	44,571	45,332	
STR	31,519	12,882	26,150	22,599	16,315	27,114	26,915	19,700	33,898	41,748	46,944

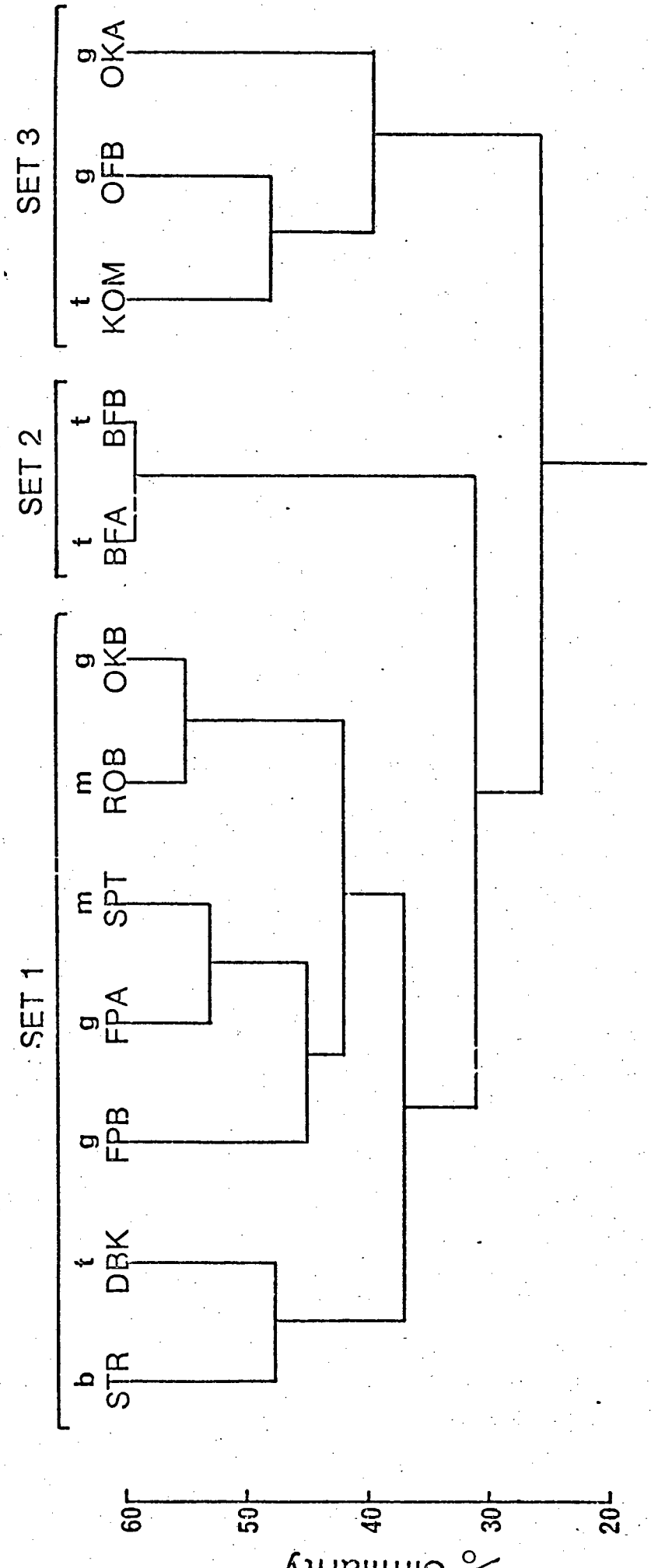


Fig. 1.37 Dendrogram based on data for all beaches.
(b = beach rock, t = Table Mountain Sandstone, g = Granite, m = Malmesbury Shale).

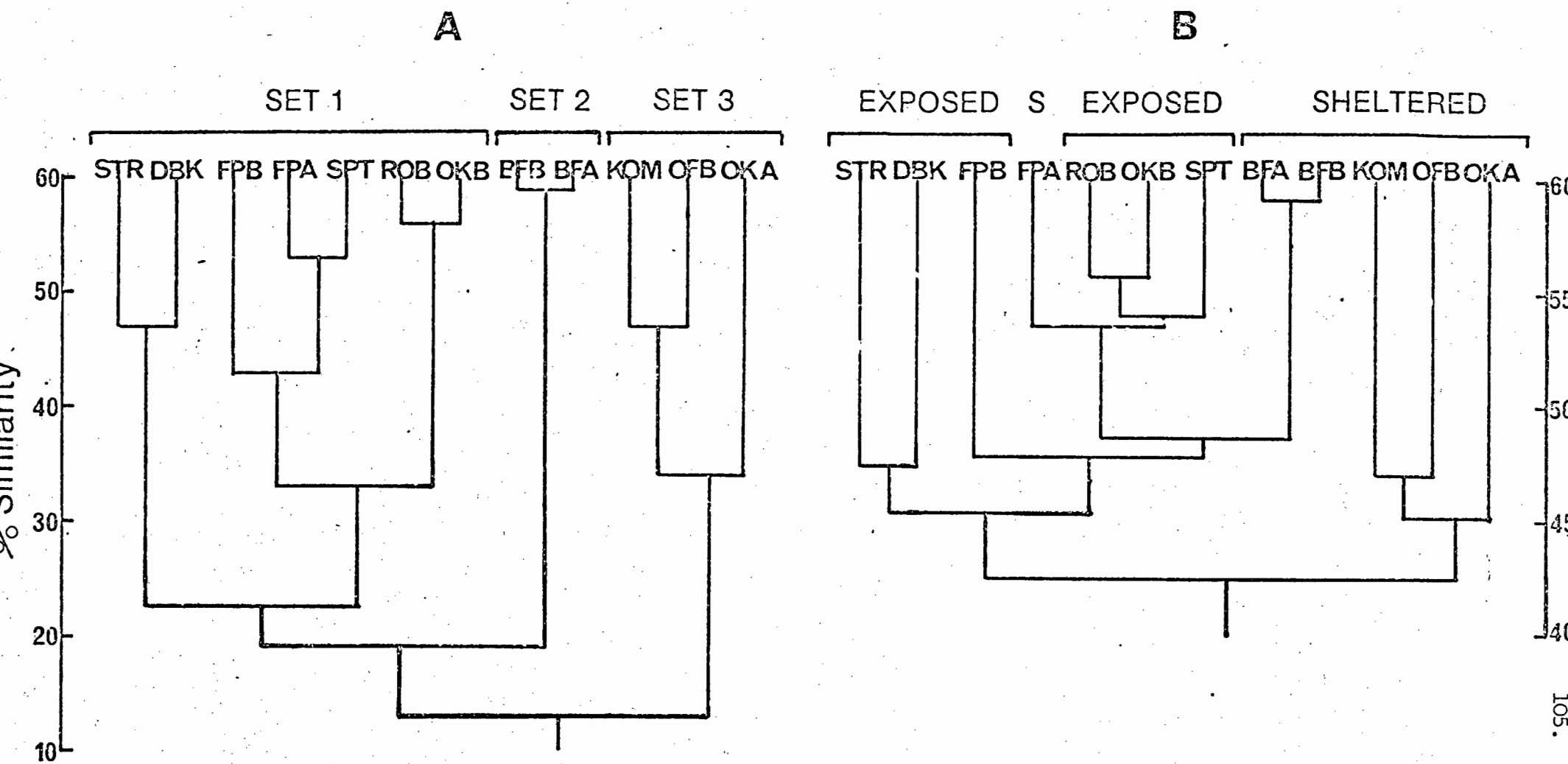


Fig. 1.38 Dendrogram based on data for all beaches using :
A Furthest-Neighbour analysis; B Nearest-Neighbour analysis.

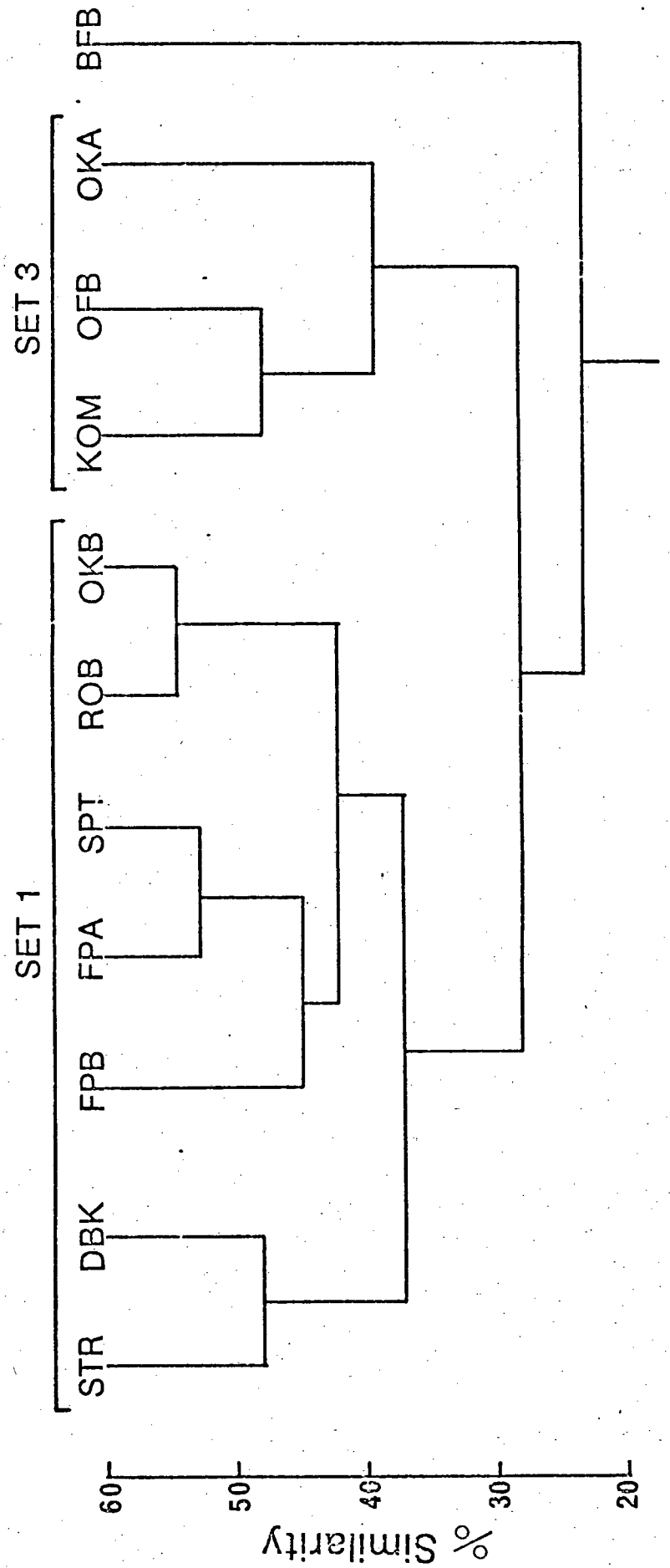


Fig. 1.39 Dendrogram based on data for all beaches except Buffels Bay A.

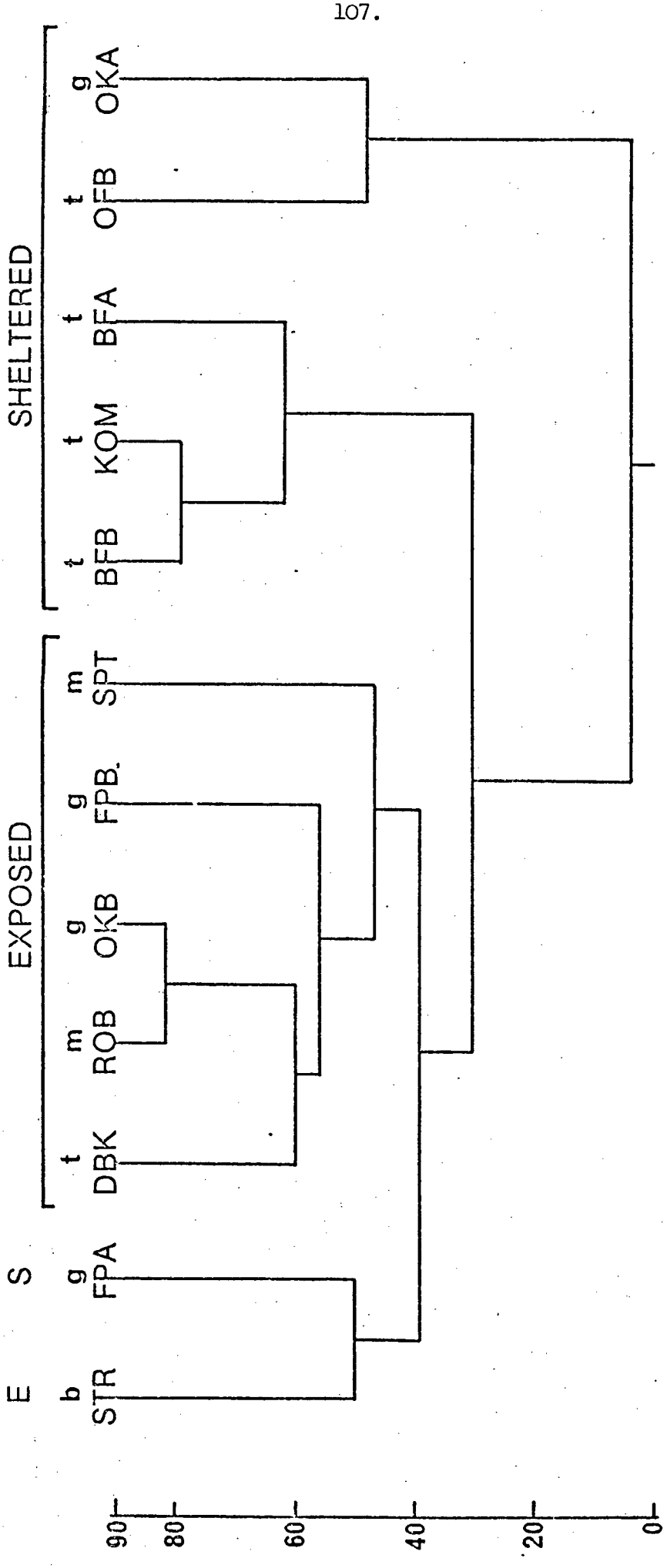


Fig. 1.40 Dendrogram on all beaches using data for filter-feeders only.
(b = beacn rock, t = Table Mountain sandstone, g = granite, m = Malmesbury Shale).

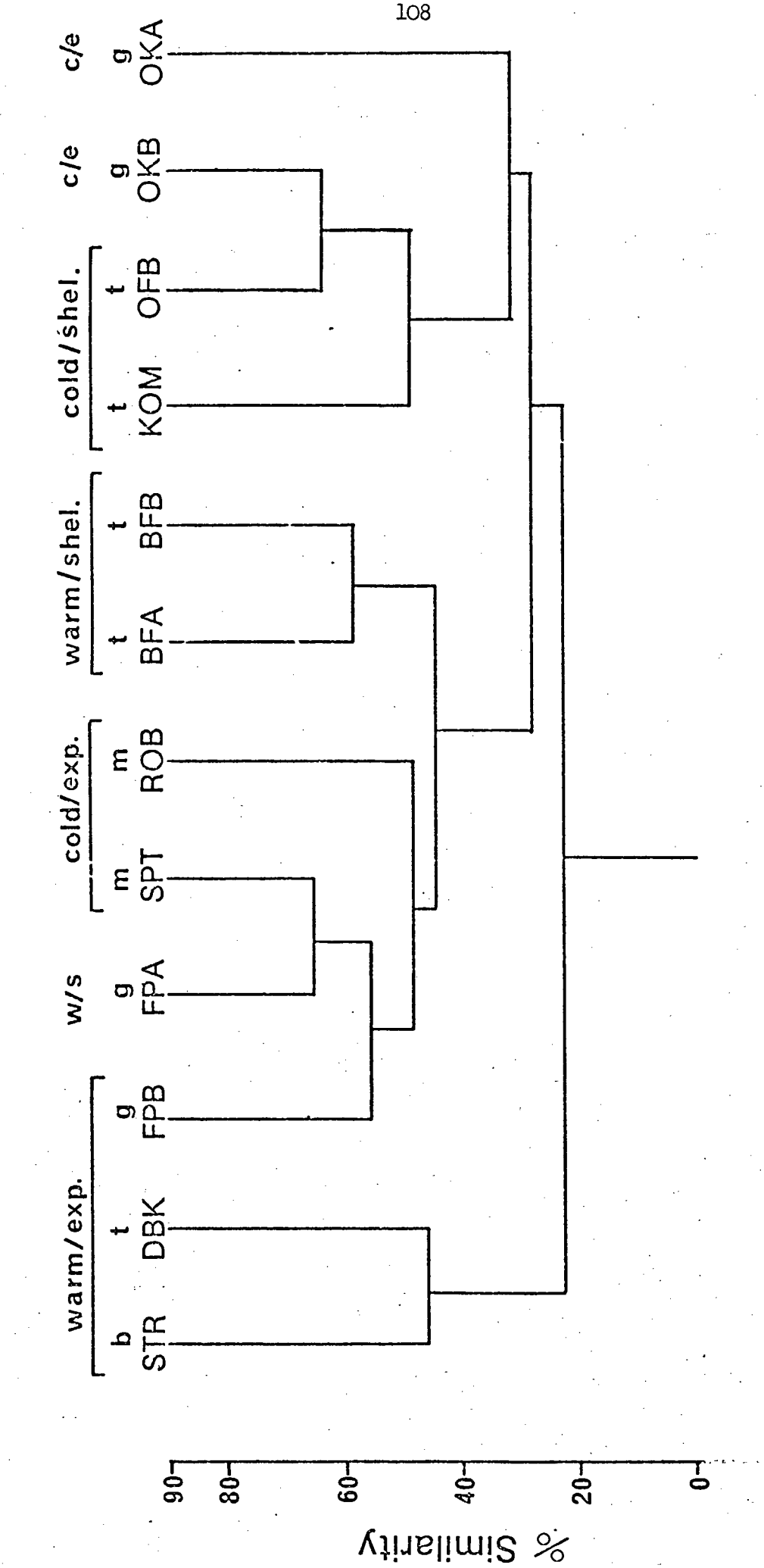


Fig. 1.41 Dendrogram on all beaches using data for algae only.
(b = beach rock, t = Table Mountain Sandstone, g = granite, m = Malmesbury shale).

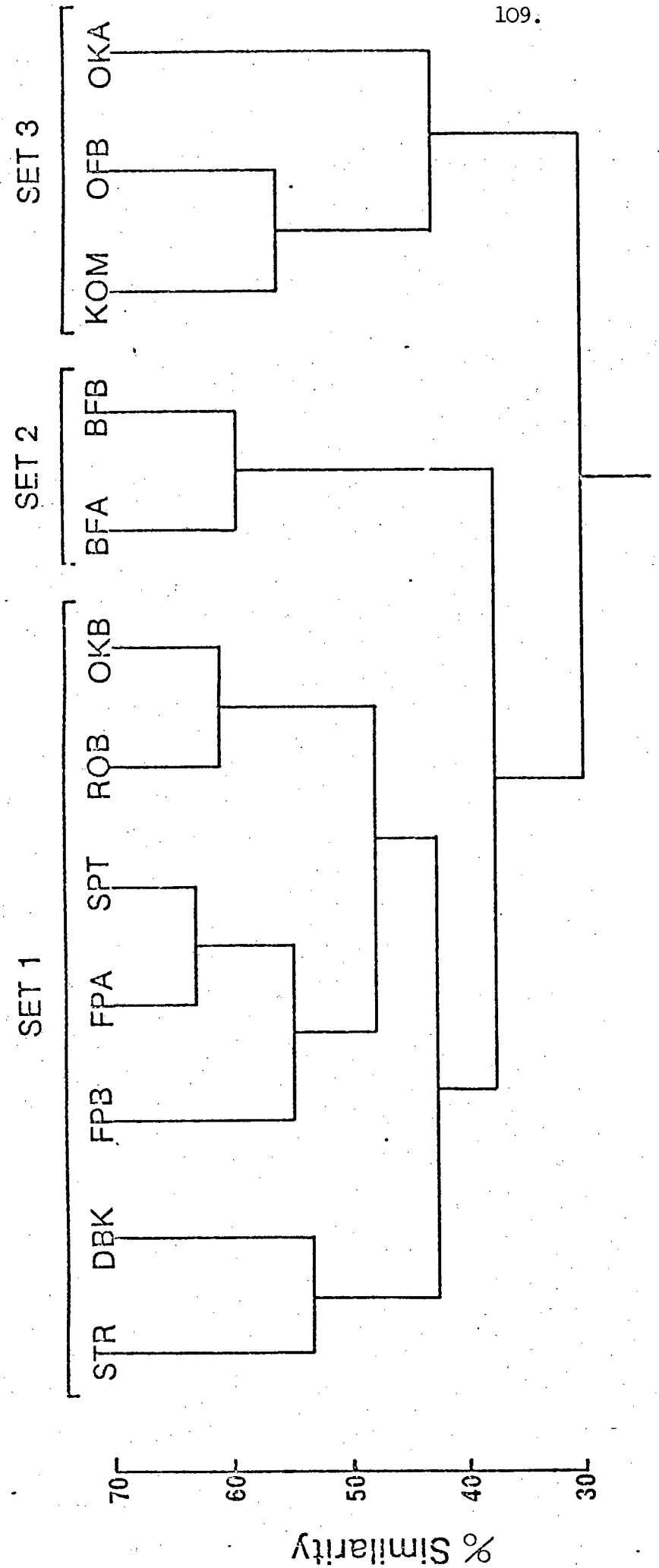


Fig. 1.42 Dendrogram on all beaches using only data on the 45 species showing highest biomass (see text).

expcsure (except for FPA). Within set 1 subdivision is on the basis of temperature. The sheltered beaches are also separated according to temperature. Due to the abnormality of BFB they form two separate sets rather than subdivisions of a single set.

(b) Analyses based on data for selected species only.

A dendrogram based on data for filter-feeders only (fig. 1.40) groups all the exposed beaches together. Strandfontein is however less closely linked than the remaining exposed beaches. This is explicable in terms of substrate conditions (see below).

The possibility of reduced algal biomass and richness on granite beaches suggested by Levyns (1924) and Isaac (1937) was examined by considering data on algae only (fig. 1.41). This reveals no correlation between algal biomass and substrate. Basically the same major sets are revealed as in the analysis based on all species (fig. 1.37) with the exception that the cold exposed beach OKB is included with the cold sheltered beaches of set 3. These sets are linked differently however and the two Buffels Bay beaches of set 2 are linked to the exposed beaches of set 1. The warm, exposed DBK/STR pair are isolated.

An analysis based on only the 45 species showing highest biomass (discussed below) shows exactly the same grouping as the dendrogram for all species but at higher levels of similarity (fig. 1.42).

2. Multi-dimensional scaling.

The results of MDSCAL using 2-dimensions are given in fig. 1.43. Stress for this analysis is 0,21, this is rated as "fair" (Kruskal and Carmone, 1969) and indicates that the configuration of these points fits the data well. As data on so many variables (or species) are involved this implies a remarkably low degree of distortion. Fig. 1.43 may be envisaged as a normal dendrogram viewed from above in 2 dimensions and facilitates an understanding of the dendrogram. The close relationship between the three sets of exposed beaches which form set 1 in the group-average dendrogram analysis on all species (fig. 1.37) are clearly revealed. Again FPA, although sheltered, is closely integrated among these exposed

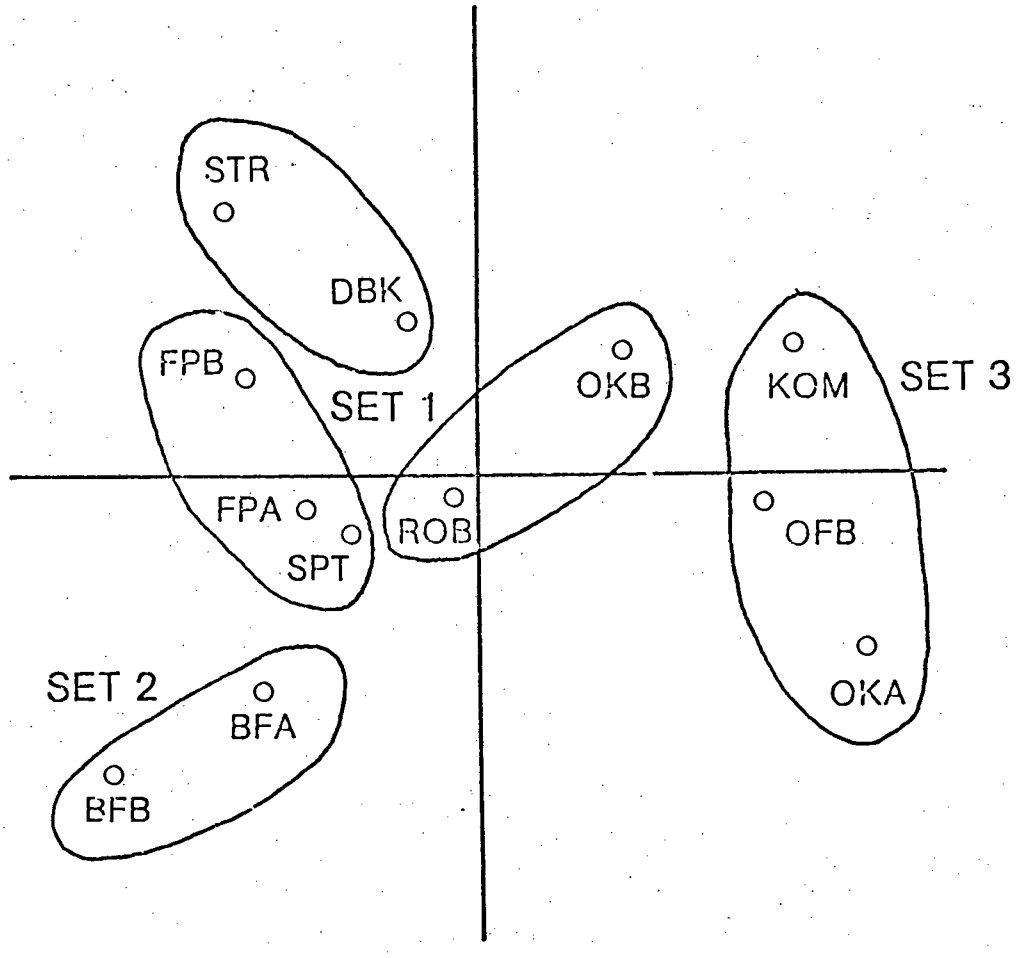


Fig. 1.43 Two-dimensional MD-SCAL ordination showing sets 1-3 derived from fig. 1.37. Stress = 0,21.

beaches. The positions of sets 2 and 3 relative to each other and the exposed beaches are interesting and confirm the isolated condition of set 2.

3. Richness. (Table 1.13)

(a) Values for the boulder beaches OKA and BFB are particularly low as these offer an unstable substrate. Furthermore the lowest values for False Bay occur at Strandfontein where the soft substrate is easily eroded (see below) and at Buffels Bay which is subjected to tongues of cold water from the Atlantic current system as described. Richness at these four beaches (OKA, BFB, BFA, STR) is found to be significantly lower than for the remaining beaches ($P < 0,05$).

(b) A comparison of west and east coast beaches shows no significant differences even if the above four beaches, which are aberrant for various reasons, are omitted. The overlap region between south and west coast biota described by Stephenson (1944) includes False Bay and the west coast as far as Kommetjie. Richness is found to be significantly higher in this overlap region than for the remaining cold beaches ($P < 0,05$).

(c) No significant difference is found between richness of igneous and sedementary beaches. Although Day (1959) found exposed beaches to be richer than sheltered beaches this was not found in the present study. Day's findings however are based on beaches in Langebaan lagoon where much less extreme conditions of exposure prevail.

4. Evenness (Table 1.13)

(a) The three beaches with unstable or easily eroded substrates (OKA, BFB, STR) show significantly higher evenness than the remaining beaches ($P < 0,01$).

(b) If these three beaches are omitted, cold (i.e. west coast) beaches show significantly higher evenness than warm (ie. False Bay) beaches ($P < 0,01$).

(c) Finally, if species are ranked according to biomass for each beach and biomass of the ten most abundant species is summed they are found to account for 90 % of total biomass on each beach. Furthermore,

if the ten species for each beach are listed, it is found that a total of only 45 species is involved. Thus 45 species (out of a total of 310) account for approximately 90 % of total biomass on all twelve beaches examined. These species, the ranks of the ten most abundant on each beach, and the percentage of total biomass they form, are given in table 1.14.

TABLE 1.13 SPECIES RICHNESS (S) AND EVENNESS (J) ON THE TWELVE BEACHES EXAMINED.

	West Coast						False Bay					
	ROB	SPT	OKA	OKB	KOM	OFB	BFA	BFB	FPA	FPB	DBK	STR
S	90	98	43	81	118	101	90	63	117	99	137	88
J	0,8819	0,8647	1,4028	1,2007	1,0660	1,0195	0,6193	1,2210	0,5792	0,6332	0,7815	1,2217

5. Information statistic and U-tests

A number of indicator species and species showing trends in abundance were revealed. The results of warm/cold beach comparisons (Table 1.15) conform with findings of Isaac (1938) and Stephenson (1944) and present distributional records (Day et al, 1970; Simons, 1976; U.C.T. records). A total of 32 species show significant trends in abundance in response to temperature. These form a mixed group of which 12 are more abundant on cold beaches and 19 are more abundant on warm beaches.

Exposed/sheltered comparisons provide only one indicator species (Table 1.16). This is Octomeris angulosa which was also found by Field and MacFarlane (1966) to be a useful indicator of exposed conditions. No indicator species for sheltered conditions are revealed. There is, however, a group of 36 species showing abundance trends in response to exposure. Almost all of these, (30 out of 36) show significantly greater biomass on exposed than on sheltered beaches. These include 25 of the 45 species with highest biomass.

TABLE 1.14 : THE TEN SPECIES SHOWING HIGHEST BIOMASS AT EACH BEACH EXAMINED

(Species are listed according to the zoogeographic affinity from east coast to west coast species. Figures indicate the biomass rank at each beach. Mean % of total biomass formed by the 10 species for each beach = 92,38 %)

SPECIES	SPT	OKA	OKB	ROB	OFB	KOM	BFA	BFB	FPA	FPB	DBK	STR	ZOOGEOGRAPHIC AFFINITY (based on Stephenson, (1944))
Caulerpa filiformis												3	East coast dying out in south coast
Laurencia flexuosa												7	Local east/south coast
Sargassum heterophyllum											9		
Perna perna										10			East-West coast dying out past Cape Point (note S. deflexa)
Plocamium corallorhiza											10	4	
Siphonaria deflexa		6											
Acanthochiton garnoti												10	South coast passing Cape Point
Bunodosoma capensis			6	9					6				
Gelidium pristoides			4			5	7			5	5	5	
Patella cochlear		1		3	4		9	10			8		
P. oculus							10	3					
Bifurcaria brassicaeformis	1			1			1	1	1	2			South-West local
Centroceras clavulatum					10								Ubiquitous
Octomeris angulosa	8		2	2			6			1	2		
Parechinus angulosus								8					(note P. granularis (higher biomass on West coast), an P. barbara, Pyura stolonifera (higher biomass in False Bay).
Patella barbara							8		7			2	
P. granularis	5		10	10		10						9	
Pseudoneries variegata	10			8						9			
Pyura stolonifera									9	8	1	6	
Tetraclita serrata			8	7		7	4	6	10		4	1	
Ulva sp.	3				9	9				7			
Balanus algicola										6			West-South coast (ie. 'ubiquitous' in Cape Peninsula).
Gigartina radula		8				4			3		3		
Helcion pectunculus								7					
Oxystele variegata		2					5	2					
Plocamium cornutum										3			
Porphyra capensis					2	8							
Pseudactinia flagellifera								9					
Splachnidium rugosum					3								

(Continued)

TABLE 1.14 (Continued)

SPECIES	SPT	OKA	OKB	ROB	OFB	KOM	BFA	BFB	FPA	FPB	DBK	STR	(Stephenson's (1944) categories)
Aeodes orbitosa		9	7		8	1							West coast passing Cape Poi
Champia lumbricalis			3	5	1								
Chromytilus meridionalis	7												(biomass higher on West coa
Gigartina stiriata	6	10	5	6	5	3			2		6		of Peninsula, with exceptic
Gymnogongrous dilatatus		3											of G. stiriata).
Patella granatina		5			7	2							
Bifurcariopsis capensis							2						
Burnupena papyracea									8				*
Jania sp.									5				(Biomass high only in False Bay)
Tapes corrugatus												8	
Arthrocardia sp.	2	4			6		3	4	4		7		(Biomass high on bo
Aulacomya ater	4		1	4						4			coasts of Peninsul
Burnupena delalandii	9							5					
Cladophora capensis			9										(High biomass only
Dicurella sp.		7											on west coast of
Gigartina scabiosa						6							Peninsula)
% of Total biomass formed by these 10 spp.	90,97	89,05	93,51	94,91	92,72	91,02	95,79	92,78	91,57	95,35	91,99	88,92	

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TABLE 1.15 : INDICATOR SPECIES AND SPECIES SHOWING BIOMASS TRENDS IN RESPONSE TO TEMPERATURE AT 95 % CONFIDENCE LEVEL.

(I-sp = good indicator species; B signifies greater biomass on exposed (E) or sheltered (S) beaches. * denotes one of the 45 spp. showing highest biomass).

SPECIES	Presence/ absence	Biomass	Conclusions
ALGAE			
* Aeodes orbitosa	+	+	I-sp-C
* Champia lumbricalis	-	+	B - C
* Cladophora capensis	-	+	B - C
* Gigartina stiriata	+	-	Poor I-sp-C
* Gymnogongrous dilatatus	+	+	I-sp-C
* Porphyra capensis	-	+	B - C
PLATHYHELMINTHES			
Polyclad sp.	-	+	B - C
POLYCHAETA			
Lumbrinereis coccinea	-	+	B - W
Lysidice natalensis	-	+	B - W
Perenereis capensis	+	+	I-sp-W
Platenereis dumerillii	-	+	B - W
Dodecaceria pulchra	-	+	B - C
Pomatoleios kraussi	+	+	I-sp-W
ISOPODA			
Dynamenella australis	-	+	B - C
D. dioxus	+	+	I-sp-W
Iais pubescens	+	-	Poor I-sp-W
Paridotea ungulata	+	+	I-sp-C
AMPHIPODA			
Hyale diastema	+	+	I-sp-W
H. grandicornis	+	+	I-sp-C
TANAIDACEA			
Leptochelia barnardi	+	+	I-sp-W
BRACHYURA			
Plagusia chabrus	-	+	B - W
PELECYPODA			
Thecalia concamerata	+	+	I-sp-W

SPECIES	Presence/ absence	Biomass	Conclusions
GASTROPODA			
Burnupena lagenaria	+	+	I-sp-W
Crepidula porcellana	+	+	I-sp-W
Oxystele sinensis	+	+	I-sp-W
* O. variegata	-	+	B - W
* Patella barbara	-	+	B - W
* P.oculus	-	+	B - W
Siphonaria capensis	+	-	Poor I-sp-C
Tricolia neritina	-	+	B - W
ECHINOIDEA			
* Parechinus angulosus	-	+	B - W
TUNICATA			
* Pyura stolonifera	+	+	I-sp-W

TABLE 1.16 : INDICATOR SPECIES AND SPECIES SHOWING BIOMASS TRENDS IN RESPONSE TO THE DEGREE OF EXPOSURE AT 95 % CONFIDENCE LEVEL.

(I - sp = Good indicator species; B signifies greater biomass on exposed (E) or sheltered (S) beaches.

* denotes one of the 45 spp. showing highest biomass.)

SPECIES	Presence/ absence	Biomass	Conclusions
ALGAE			
* Aeodes orbitosa	-	+	B - S
* Arthrocardia sp.	-	+	B - E
* Bifurcaria brassicaeformis	-	+	B - E
* Champia lumbricalis	-	+	B - E
* Cladophora capensis	-	+	B - E
* Gelidium pristoides	-	+	B - E
* Gigartina radula	-	+	B - E ?
* Gymnogongrous dilatatus	-	+	B - S
* Plocamium corralorhiza	-	+	B - E
* P. Cornutum	-	+	B - E
* Pterosiphonia clorophylla	-	+	B - E ?
* Ulva sp.	-	+	B - E
PORIFERA			
Hymeniacedon perlevis	-	+	B - E
ANTHOZOA			
* Bunodosoma capensis	-	+	B - E
POLYCHAETA			
Euphrosine capensis	-	+	B - E
* Pseudonereis variegata	-	+	B - E
Syllis variegata	-	+	B - E
CIRRIPEDIA			
* Balanus algicola	-	+	B - E
B. maxillaris	-	+	B - E
* Octomeris angulosa	+	+	I - sp. - E
* Tetraclita serrata	-	+	B - E
ISOPODA			
Dynamenella australis	-	+	B - E
D. huttoni	-	+	B - E

Contd./

TABLE 1.16 (continued)

SPECIES	Presence/ absence	Biomass	Conclusions
AMPHIPODA			
Paramoera capensis	-	+	B - E
AMPHINEURA			
* Acanthochiton garnoti	-	+	B - E
PELECYPODA			
* Aulacomya ater	-	+	B - E
* Choromytilus meridionalis	-	+	B - E
* Perna perna	-	+	B - E
GASTROPODA			
Fissurella mutabilis	-	+	B - E
* Patella cochlear	-	+	B - E
* P. granatina	-	+	B - S
* P. granularis	-	+	B - S
Pyrene Kraussi	-	+	B - E
Thais dubia	-	+	B - S
Tricolia capensis	-	+	B - S
TUNICATA			
Pyura stolonifera	-	+	B - E

DISCUSSION

Although physical conditions set the basic pattern of species distribution and biomass, biotic factors may be expected to have an often marked influence. The influence of Patella cochlear on algal richness and biomass is profound and has been discussed previously (p.73). Likewise a possible relationship between filter-feeder biomass and carnivore biomass has been suggested (p.81). It seems likely that grazing effects may generally be important (c.f. Castenholtz, 1961; Randall, 1961; Southward, 1956; Branch, 1971; Dayton, 1971, 1975; John and Pople, 1973), see chapter 5. Carnivore/prey interactions (eg. Connell, 1972; Dayton, 1975; Menge, 1976; Menge and Sutherland, 1976) and competition for space between filter-feeders and algae (eg. Paine, 1971a) may also have locally important modifying effects on the basic community structure.

The present study is however concerned with establishing how physical factors determine the basic structure of rocky intertidal communities and with the interactions of effects due to different factors. A number of studies have been carried out on the isolated effects of temperature, exposure and substrate as described above. The entire beach biota is generally considered in exposure studies, but many of the investigations of substrate and some of the temperature studies have been autecological. Furthermore, few of these studies have been carried out on a quantitative basis. Interactions of the effects caused by different factors may be very complex and indeed these factors may influence each other directly (eg. substrate and exposure).

The dendrograms provided give a quantitative basis for comparison of beach communities. They also reveal some of these interactions as effects on the biota as a whole. Substrate effects are limited and are overridden by both temperature and exposure effects. When either of these two factors was excluded from analysis, grouping occurred on the basis of the other. So cold beaches were grouped according to exposure (fig. 1.34A), exposed beaches according to temperature (fig. 1.35A), etc. Analyses of beaches with the same substrates (figs. 1.36A, B) indicate exposure to be the primary factor controlling grouping. Consequently in the dendrogram for all twelve beaches we find the exposed and the sheltered beaches to be grouped

separately and roughly subdivided into groups of cold-sheltered, warm-sheltered etc. (fig. 1.37).

Temperature

Considering temperature first it is apparent from Table 1.16 that the biota is mixed and may validly be divided into cold and warm water favouring forms. Only 17 species were found to be exclusive to one or other side of the Peninsula. (Table 1.15) and some species previously categorized by Stephenson (1944) on this basis do in fact appear on both coasts of the Peninsula. Where this occurs, however, the species concerned is usually restricted to one or two beaches on the inappropriate coast and is present at low biomass. Due to the limited number of beaches (ie. small sample size) on each coast, many such species do not show abundance trends when subjected to the Mann-Whitney U-test. Supplementary data from a larger number of beaches would probably yield positive results for this test for many more species. Nevertheless 32 species did reveal abundance trends in response to temperature. These include both cold water (12 species) and warm water (20 species) favouring forms.

These conclusions are indirectly supported by the data in Table 1.14. These data concern the 45 species which between them constitute approximately 90 % of biomass on all twelve beaches. They all fit well into the regional categories allocated to them by Stephenson (1944). This indicates that where they do occur outside their regional categories they form only a small percentage of total biomass. A further 10 of these 45 species are unclassified by Stephenson (1944). These fall into three goups:

1. 4 species which are more important in False Bay - these species all show a distribution around both sides of the Cape Peninsula according to present records (Day et al, 1970; Simons, 1976; U.C.T. records). The biomass patterns shown in this study are probably due to the limited number of beaches examined.

2. 3 species which are important on both sides of the Peninsula - this agrees with present distributional records.

3. 3 species which are important only on the west coast - all of these have a distribution from South West Africa to Cape Agulhas (Simons, 1976). A greater significance on the west coast is therefore to be expected.

A higher species richness within the area of overlap of the west and south coast biota might be expected. It is interesting therefore that there is no significant difference in the means of species richness on the east and west sides of the Peninsula. Stephenson (1944) however considered this overlap to extend up the west coast of the Peninsula as far as Kommetjie (see description of study area p. 7).If Olifantsbos and Kommetjie are therefore grouped with the False Bay beaches richness is significantly higher than for the remaining west coast samples ($P < 0,05$). Low richness within False Bay was found at Strandfontein and Buffels Bay B, due to substrate conditions (see below), and also at Buffels Bay A. Buffels Bay was the most southerly of the areas sampled and lies only 5-6 km north of Cape Point. Extension of tongues of cold water into False Bay as far north as Buffels Bay occur at irregular intervals (Atkins, 1970). This may result in sudden fluctuations in water temperature. Such fluctuations may be unfavourable for stenothermal species leading to a reduction in species richness.

Total beach biomass shows no significant trends in response to temperature, despite the temperature associated increase in richness. As this overlap region represents the extreme limits of distribution for many species from both the overlapping biota they are often present at very low biomass. This is confirmed by the higher evenness of cold beaches outside the overlap region. Although richness is greater in False Bay, most species are present at very low biomass resulting in domination of the communities by relatively few species and lowered evenness.

The importance of Cape Point as a primary dividing point between the south and west coast biota and of False Bay and the southern Atlantic coast of the Peninsula as an area of overlap are thus confirmed on a quantitative basis. The influence of temperature on a community level therefore, appears to be concerned with species composition and richness and to a lesser extent with biomass trends of some species.

Exposure

Richness and species composition of the communities investigated may be explained in terms of temperature effects. The degree of wave exposure has an excluding effect on only one species (Octomeris angulosa, Table 1.16) and so interferes minimally with the basic patterns of species composition established by temperature. However, a species need only be represented by a single individual to be present in the community. Certain key species may be present at very low biomass and still perform functions critical to other species or even to the community as a whole. In the absence of detailed studies on the biology of most of these species however it is reasonable to assume that actual abundance is more important than the mere presence or absence of a species. The Czekanowski coefficient yields dendrograms based on biomass scores. These indicate that exposure is the overriding abiotic factor in structuring the community (fig. 1.37). Exposure must therefore strongly influence the actual biomass of species though not necessarily their presence or absence. This was found to be true for some 36 species which showed abundance trends in response to the degree of exposure (Table 1.16). Although this is a small fraction of the total number of species recorded it includes 25 of the 45 species showing highest biomass. The degree of exposure thus influences the biomass of species forming a large proportion of total biomass on all twelve beaches. The importance of these species is brought out most clearly by the dendrogram based on data for these 45 species only (fig. 1.42) which reveals exactly the same grouping (at higher levels of similarity) as data for all species (fig. 1.37). Of the 36 species showing abundance trends in response to exposure 30 have a higher biomass under exposed conditions resulting in significantly higher total biomass on exposed beaches ($P < 0,05$).

This implies that shelter preferring species can occur on exposed beaches at high biomass. Species which prefer exposed conditions however can extend into sheltered areas only at low biomass. This in turn suggests that the biota as a whole is geared to exposed conditions and has biological and ecological implications for the species involved which may warrant further investigation. For example, the limpet Patella cochlear is one of these species which has been studied in greater detail. It was found here to show higher biomass on exposed shores and

consequently the cochlear zone is poorly developed on some sheltered beaches (p.77). This is in agreement with the findings of Branch (1975a) and is related to a very high tenacity of the species (Branch and Marsh, 1978).

The degree of exposure also has a significant influence on three of the trophic compartments as described above (see p.45). The domination of exposed shores by filter-feeders is particularly important and results in a different pattern of trophic dominance compared with sheltered beaches. This may be expected to have a profound influence on energy flow through the community as a whole. Despite this domination by filter-feeders exposed beaches do not show a significantly lower evenness than sheltered beaches. This may be largely due to the fact that the bulk of filter-feeder biomass is generally made up by several species. This and the large fraction of biomass made up by algal species result in an evenness similar to that of sheltered beaches.

To summarize the effects of exposure it may be concluded that while temperature influences the actual species composition of these communities, the biomass of most of the species forming the bulk of intertidal biomass is influenced by the degree of exposure. This results in a different pattern of trophic dominance and a higher total biomass on exposed beaches. Because of this, exposure assumes the dominant role in the structuring of these communities leading to dendrogram grouping based primarily on exposure effects.

Indirect evidence from this study however, suggests the importance of local current conditions and the biological history of any particular beach. Both Robben Island and Seapoint are exposed shale beaches on the cool Atlantic coast. Despite this similarity of physical conditions they are not directly linked in a dendrogram analysis (fig. 1.37). There are important differences in species biomass at Robben Island and Seapoint. The trophic compartment profiles (figs. 1.18, 1.19) indicate a different pattern of trophic dominance on the two beaches. The domination of the middle and upper regions of Robben Island by filter-feeders is due to an extremely high biomass of Tetraclita serrata.

Seapoint has the lowest filter-feeder biomass among the exposed beaches (Table 1.6). Although T. serrata forms much of filter-feeder biomass in the upper balanoid its biomass is particularly low (Table 1.11).

Robben Island is situated in the middle of Table Bay and this effect may be due to a different pattern of current conditions at Robben Island and Seapoint resulting in a different larval input (c.f. Behrens Yamada, 1977). In the absence of more than indirect hydrographic evidence (Sillington pers. com., 1979) however, this remains a tentative suggestion. As Lewis (1964) has pointed out direct evidence on the significance of current patterns is difficult to obtain but indirect evidence based on density, or in this case biomass, measures may be inferred. Although only one species has been considered here it is an important one and may indicate an important principle.

Substrate

No grouping of beaches according to substrate was found in any of the similarity analyses. Likewise some predicted effects of substrate were not found to occur. For example there was no decrease in algal biomass on granite beaches (Table 1.7) although this was found by Levyns (1924) and Isaac (1937). The dendrogram based on data for algae only (fig. 1.41) does not indicate any trend of species composition or biomass in response to substrate type.

Despite the absence of generalised substrate effects on beach communities as a whole certain specific effects were found. Instability of substrate at the two boulder beaches Buffels Bay B and Oudekraal A was found to result in a significant reduction in species richness and total biomass on these beaches (Tables 1.6, 1.13). As may be expected this was most marked for sedentary forms such as algae and filter-feeders (p. 43). Also at Buffels Bay B Patella cochlear was much less abundant than P. oculus and the more mobile Oxystele variegata. Although this beach is sheltered and P. cochlear favours exposed conditions (Branch, 1975a) this may also be explained by growth rates. P. cochlear has a much slower growth rate than P. oculus (Branch, 1974) which may result in low abundances on an unstable substrate.

Similarly Strandfontein has a very soft and rapidly eroded substrate and is the only beach where a distinct cochlear zone does not occur. P. cochlear is replaced here by P. barbara which also dominates the lower balanoid. Again P. barbara has a much more rapid growth rate (Branch, 1974). The friable nature of the rock at Strandfontein also results in a reduction in species richness and the absence of dense beds of filter-feeders. Although Tetraclita serrata is abundant it occurs as scattered clumps of individuals and is not as conspicuously dominant as in the upper zones of other exposed beaches.

Algal biomass at Strandfontein is the lowest for all except the two boulder beaches. This may be due in part to the nature of the substrate. The fact that Strandfontein is surrounded by long stretches of sandy beach may also have an impoverishing effect, due to sand scouring. This was found for algae on a similarly isolated rocky beach in New Hampshire by Daly and Mathieson (1977). Caulerpa filiformis, however, is resistant to the effects of sand movements (Simons, 1976) and is abundant at Strandfontein forming 32 % of total algal biomass.

Further effects of the substrate at Oudekraal A, Buffels Bay B and Strandfontein are reflected in a significantly higher evenness than on the other beaches ($P < 0,01$). Substrate conditions on these three beaches are unsuitable for any particular biotic forms. While some species occur at higher biomass than on other beaches no particular species dominate the beach so that evenness is relatively high.

The main effects of substrate were thus found to be impoverishment of biota due to instability or erosion of the substrate. This particularly affects sedentary or slow growing forms and is associated with a decrease in species richness and an increase in the evenness of the community. Unstable substrates also have specific effects on the ecology of Patella species. On such beaches P. cochlear becomes less abundant and fast growing species such as P. oculus and P. barbara form a larger proportion of herbivore biomass. On the whole however these effects are overridden by those of exposure and substrate.

The pattern which emerges may be summarized as follows: temperature effects establish the framework of species composition on different beaches as well as influencing the biomass of a few species.

Exposure has an overriding influence however by affecting the biomass of many of the species which dominate biomass on the beaches examined. Exposure also has a direct influence on the trophic structure of these communities and thus the basic patterns of energy flow through them. Thus beaches may be defined firstly according to the degree of exposure they experience and then subdivided according to the temperature regime they experience. Within this framework substrate has specific effects concerned mainly with instability on friability leading to impoverishment of the community. Also the shape of the beach, determined largely but not exclusively, by substrate, influences herbivore biomass (see p. 51). Beyond this however the actual rock type does not appear to have any important general effects.

SUMMARY

1. It is difficult to consider more than a few major species when subjectively assessing the effects of physical factors. This is even more difficult if interactions between the effects of a number of factors are to be considered. The use of a similarity analysis has the advantage that the overwhelming amount of information derivable from beach transects may be analysed on a quantitative basis and interactions of a number of variables may be considered.

2. Beaches were found to group together on the basis of similarity of conditions of primarily exposure and secondarily temperature. Temperature was found to primarily influence species richness and composition. Exposure affects the biomass of a large number of the most important species and thus has an overriding influence on community structure. The degree of wave exposure also influences trophic structure as previously discussed.

3. Limited local and autecological effects of substrate were found. These particularly concerned instability of substrate causing a reduction in species richness or biomass. Any overall effects of substrate on community structure were masked by other factors.

4. An additional influence on beach communities in the form of current systems and the biological history of the beaches is suggested.

5. The ten species showing highest biomass on each beach formed about 90 % of total biomass. A total of only 45 species is involved when all 12 beaches were considered.

6. The importance of Cape Point as a primary dividing point between the west and south coast biota, and of False Bay and the west coast of the Peninsula as far north as Kommetjie as an overlap region between these two biota is confirmed on a quantitative basis.

PART II

CHAPTER 5 : SEASONAL VARIATIONS IN BIOMASS, ZONATION AND CALORIFIC VALUE OF INTERTIDAL ALGAE

INTRODUCTION

This section represents the second phase of a base-line study of intertidal conditions in the Cape Peninsula. The first phase entailed an investigation of general conditions of zonation and trophic organization on twelve beaches. This included an examination of spatial variation in intertidal communities and of the influences of wave exposure, temperature and substrate on these communities. Important temporal variations in these communities may also be expected. In this second phase an investigation is made into seasonal variations in the algal community of Dalebrook beach in False Bay and into population fluctuations in two gastropod species (Chaps. 6 and 7).

Some primary production is carried out in the intertidal zone by attached diatoms and considerable energy is imported into the system in the form of plankton and suspended matter. Macroalgae are among the chief primary producers present and are an important source of energy for the system. They also extensively modify the environment by their presence providing shelter for often very rich epifaunas. The energy fixed by macroalgae may be utilized in the intertidal system by direct grazing or exported into the marine system by the erosive and dissolving effects of the sea (eg. Khailov and Burlakova, 1969).

In order to understand the potential for energy fixation by algae and the availability of this energy to primary consumers the answers to a number of fundamental questions are required. Information is needed as to which species are present and whether these vary during the year. Details are needed of species zonation and standing crop throughout the year. Finally some evaluation of the energetic quality of the algal standing crop is required.

Seasonal variations of intertidal algal standing crop have been reported by a number of authors including Batham (1956), Cronwell and

Moore (1938), Underwood (1973) and Bokenham and Stephenson (1938). They are to be expected in temperate climates where there are seasonal variations in factors influencing growth such as sunlight, air and sea temperatures. Late summer blooms of the dominant lower balanoid species Gigartina radula at Dalebrook are obvious but no quantitative work has been done on this. Little is known about the periodicity or regularity of these blooms or of seasonal variations in the standing crop of other species and thus of potential food available to primary consumers.

Similarly there is little knowledge of seasonal changes of zonation such as those reported by Mshigeni (1977), Lawson (1957) and Knight and Parke (1931; cited by Lawson, 1957). This too may be a factor of some importance to primary consumers. Despite extensive evidence of seasonal changes in the chemical composition of algae the evidence regarding seasonal changes in their calorific content is conflicting. Paine and Vadas (1969) found no seasonal changes in the calorific value of algae. Mann (1972) however predicted such changes and they were subsequently recorded by Himmelmann and Carefoot (1975) and Breton-Provencher and Cardinal (1976). Data on this important aspect of algal seasonality however remain limited. The possibility of such changes is of particular significance to herbivores as this involves changes in the energetic quality of the algae.

The present study was initiated to investigate these key problems:

1. Do species composition and dominance remain constant throughout the year?
2. Are there regular changes in the biomass, zonation or calorific content of the most abundant species?
3. How are such changes, if any, related to variations in growth-influencing abiotic factors?

Study Area

Dalebrook is an exposed beach in the warm water False Bay area (34° 07'S, 18° 27'E). The beach consists of a long (70 m) gently sloping platform of sandstone separated by a narrow gulley from a large table-like rock island in the lower cochlear zone. Beyond this rock the sub-tidal fringe gradually drops away to a depth of 11 m about 100 m off-shore. The upper littoral zone is marked by a second platform raised approximately 0,3 m above the main beach and bounded upshore by a series of large rocks marking the MHWS level (see fig. 1.28).

The lower cochlear island is densely populated by Patella cochlear and there are few algae present due to grazing pressure (see p.73). However the thick growths of Arthrocardia sp. and Pterosiphonia cloiophylla fringe the lower parts of this zone. In the mid-cochlear density of P. cochlear declines and these species lose their dominance being joined by clumps of Gelidium pristoides and Ulva sp. along with some Centroceras clavulatum and Gigartina stiriata. The lower balanoid zone is dominated by Gigartina radula with smaller quantities of G. pristoides, Ulva. sp. and C. clavulatum. G. radula and C. clavulatum drop out towards the mid-balanoid zone which is densely covered with G. pristoides and Ulva sp. The upper balanoid is dominated by the barnacle Tetraclita serrata amongst which scattered plants of G. pristoides, Ulva sp. and Chaetangium erinaceum grow. The upper platform which forms the Littorina zone, was originally bare of macrophytic algae but along with parts of the upper balanoid became colonized by Porphyra capensis during the course of field work.

METHODS AND MATERIALS

Initial surveys revealed that although some 24 species of algae are present in the study area approximately 84,8 % of algal biomass is attributable to 9 species. These are Arthrocardia sp., Centroceras clavulatum, Chaetangium erinaceum, Gelidium pristoides, Gigartina radula, G. stiriata, Porphyra capensis, Pterosiphonia cloiophylla and Ulva sp. Furthermore 63,5 % of this, or 54 % of total biomass is formed by the four conspicuous species Ulva sp., Gelidium pristoides, Gigartina radula and Porphyra capensis.

These 9 species were monitored for zonation and biomass during spring low tides every six weeks for a period of 15 months, from September 1976 to December 1977. The biomass of each species varies greatly within the different zones occupied. To allow for this heterogeneity the beach was mapped and divided into 11 zones on the basis of algal species dominance (fig.2.6A). Triplicate samples of algae were taken at six weekly intervals in each zone by scraping 0,25 m^2 quadrats laid down randomly in each zone. Where distribution was markedly patchy 4 samples of 0,5 m^2 were taken. Due to its extremely clumped distribution the biomass of Porphyra capensis was derived from measures of percentage cover coupled with biomass measures from areas with 100 % cover.

Samples were subsequently sorted to species level, and dry weights obtained by drying at 60° C for a minimum of 48 hours. In all samples the 9 species under consideration constituted between 80 and 100 % of dry weight. Mean values from triplicate samples were used in subsequent calculations. Dried sub-samples were retained in sealed bottles for calorific analysis.

From these samples it was possible to monitor both biomass $.m^{-2}$ for each zone and total biomass for each species for the entire beach (calculated from the areas of zones where biomass was measured).

Calorific values were obtained using a Gallenkamp ballistic macro-bomb calorimeter, calibrated with thermochemical standard benzoic acid of known calorific value. Values for the heavily calcified species Arthrocardia sp. were corrected for endothermy following Paine (1966). The correction factor was derived separately for each month on the basis of monthly ash content. Ash free weights were obtained by heating ground samples to 500° C for a period of 5 hours in a muffle furnace.

Cross-correlation analysis

Seasonal variations in algal standing crop may correlate with seasonal variations in environmental factors. The most important of these are likely to be tidal height, light and sea temperature. Seasonal variations in air temperature occur and cover a greater seasonal

range than sea temperatures. However, as Naylor (1976) has pointed out, the importance of this is reduced in areas where low tides occur in early morning and late evening. Diurnal low tides in this area occur at 8.00 - 9.30 a.m. and air temperatures are therefore presumed to be of limited significance. Thus sunlight intensity, sea temperature and mean height of low tides are likely to be the most critical variables.

In order to examine correlations between biomass and these three environmental factors cross-correlation analyses were performed between the curves derived for biomass and the concurrent sections of the curves derived for these factors. The chief advantage of this analysis lies in the fact that the two curves may be put out of phase with one another. This is useful as a refractory period may occur between environmental changes and algal response.

Cross-correlations yield a correlation coefficient by comparing the shapes of two curves. The formula applied for zero lag is :

$$\rho_{xy} = \frac{\sum_{i=1}^{n} (x_i - \bar{x})\ (y_i - \bar{y})}{\sqrt{\left(\sum_i (x_i - \bar{x})^2 \left(\sum_i (y_i - \bar{y})^2\right)\right.}}$$ (Kendall and Stuart,1966)

Correlations for lag 1 (when one curve leads the second by an x - axis interval of one, (in this case an interval of six weeks) or lag 2 (an interval of 12 weeks) etc. may be derived. This is carried out by replacing x_i with x_{i+1}, or x_{i+2} etc. $\bar{x}$ is then calculated for $x_{i+1} - x_n$ or $x_{i+2} - x_n$ etc. and $\bar{y}$ is calculated for $y_{i+1} - y_n$ or $y_{i+2} - y_n$ etc.

Values of ρ range from -1 (perfect correlation, perfectly out of phase) to +1 (the two curves are perfectly correlated and perfectly in phase).

Generally a correlation value of 0,8 is considered a "good" correlation. In the case of biological data such as these where biomass may be influenced by all three environmental factors as well as additional environmental or biotic factors correlations well below 0,8 are to be expected.

RESULTS

1. Biomass

The nine species monitored may be divided into dominant and sub-dominant species on the basis of biomass values and the pattern of distribution within each zone. The various zones are dominated by Gigartina radula (lower balanoid), Gelidium pristoides/Ulva sp. (mid balanoid) and Porphyra capensis (upper balanoid). In the cochlear zone Arthorcardia sp. shows highest biomass but there is reason to believe that Pterosiphonia cloiophylla has a dominating effect due to its taller growth form (see below).

The bulk of total beach biomass is formed by three species which are permanently present (G. radula, G. pristoides and Ulva sp.) and by P. capensis which appeared only after the beginning of the sampling period and subsequently disappeared. Variations in this community may be divided into seasonal and non-seasonal components.

(a) Seasonal variations

Mean biomass $.m^{-2}$ for all species are given in fig. 2.1. The range of biomass during the year was large in all cases. All species showed a cyclic pattern of biomass with low levels in winter and (except for Centroceras clavulatum) one period of peak biomass per year. For P. cloiophylla and G. radula only one peak period was recorded, occurring in the middle of the sampling period. For the remaining species however the 15 month sampling period covered two peaks in the biomass cycle. All of these species showed peak biomass in the same month for 1976 and 1977.

Peak biomass occurred in spring (September-October) in the case of Arthrocardia sp. and Chaetangium erinaceum, both species showing minimum biomass towards the end of summer. Summer maxima occurred for G. pristoides (early summer), Ulva sp. and Gigartina stiriata (mid summer), P. cloiophylla and G. radula (late summer) and P. capensis (late summer/autumn). The remaining species, Centroceras clavulatum, revealed two peaks of biomass, in autumn 1977 and again in spring 1977-1978.

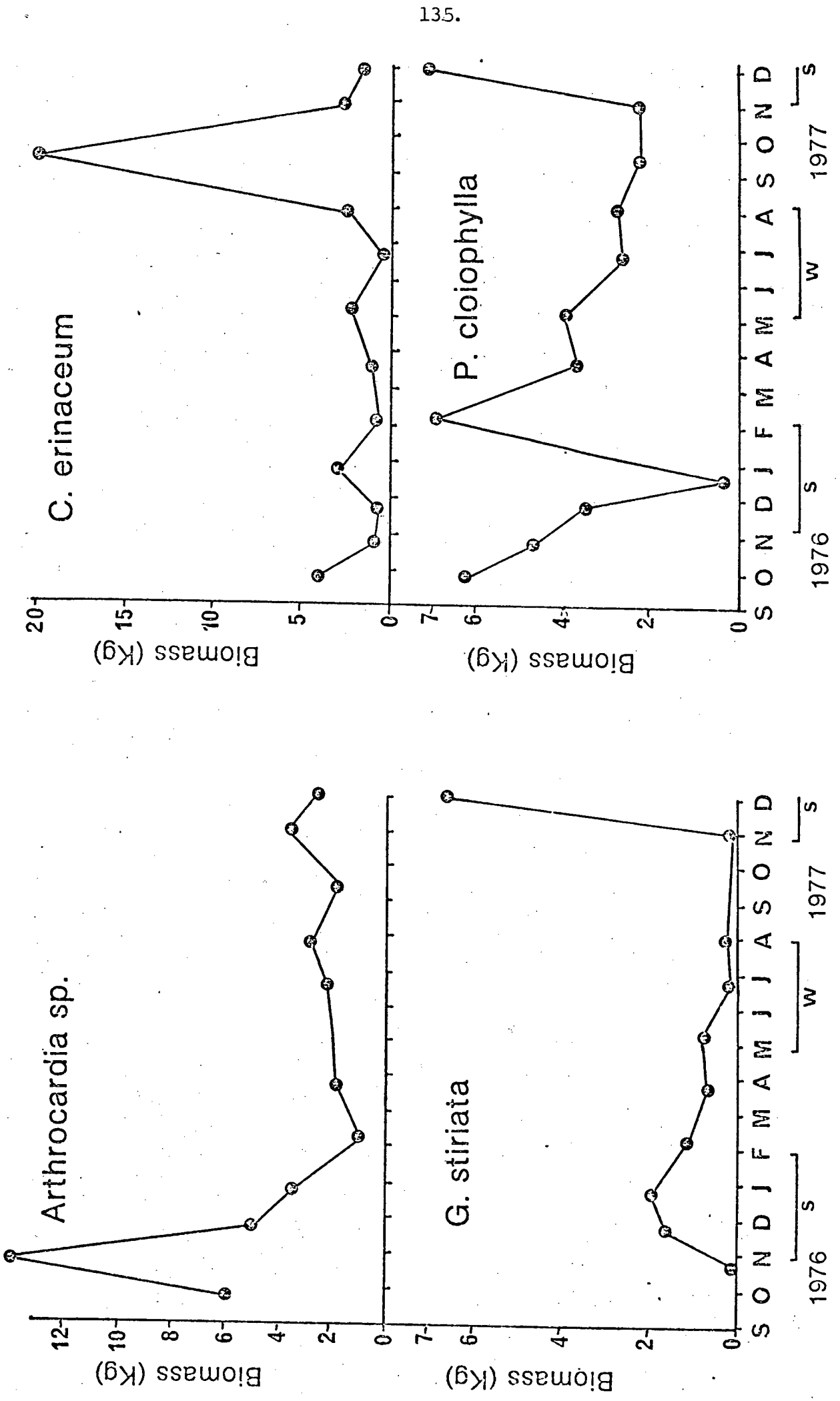
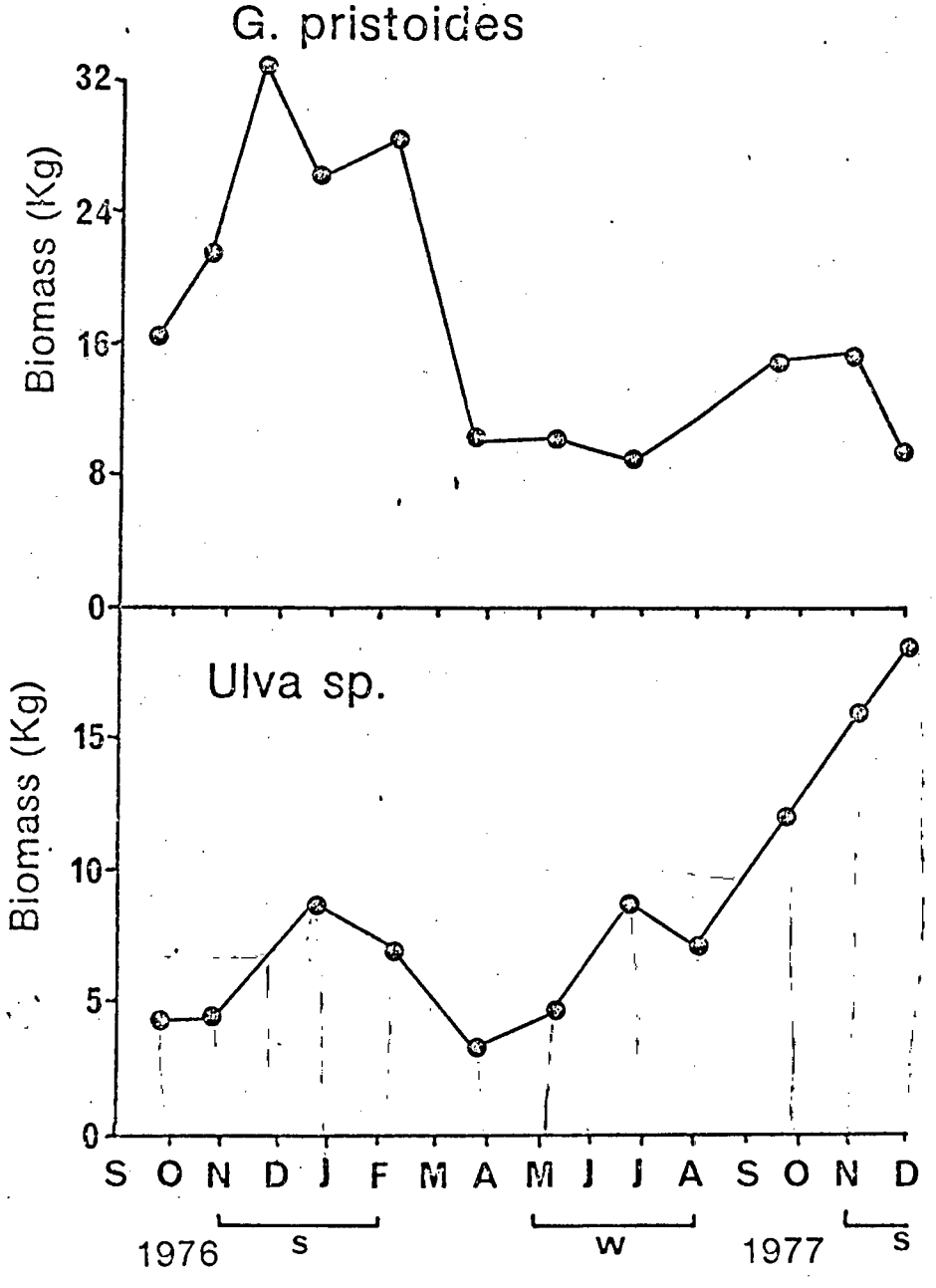


Fig. 2.1 Algal biomass fluctuations over a period of 15 months.


G. pristoides
Biomass (Kg)
32
24
16
8
0
Ulva sp.
Biomass (Kg)
15
10
5
0
S O N D J F M A M J J A S O N D
1976
s
w
1977
s

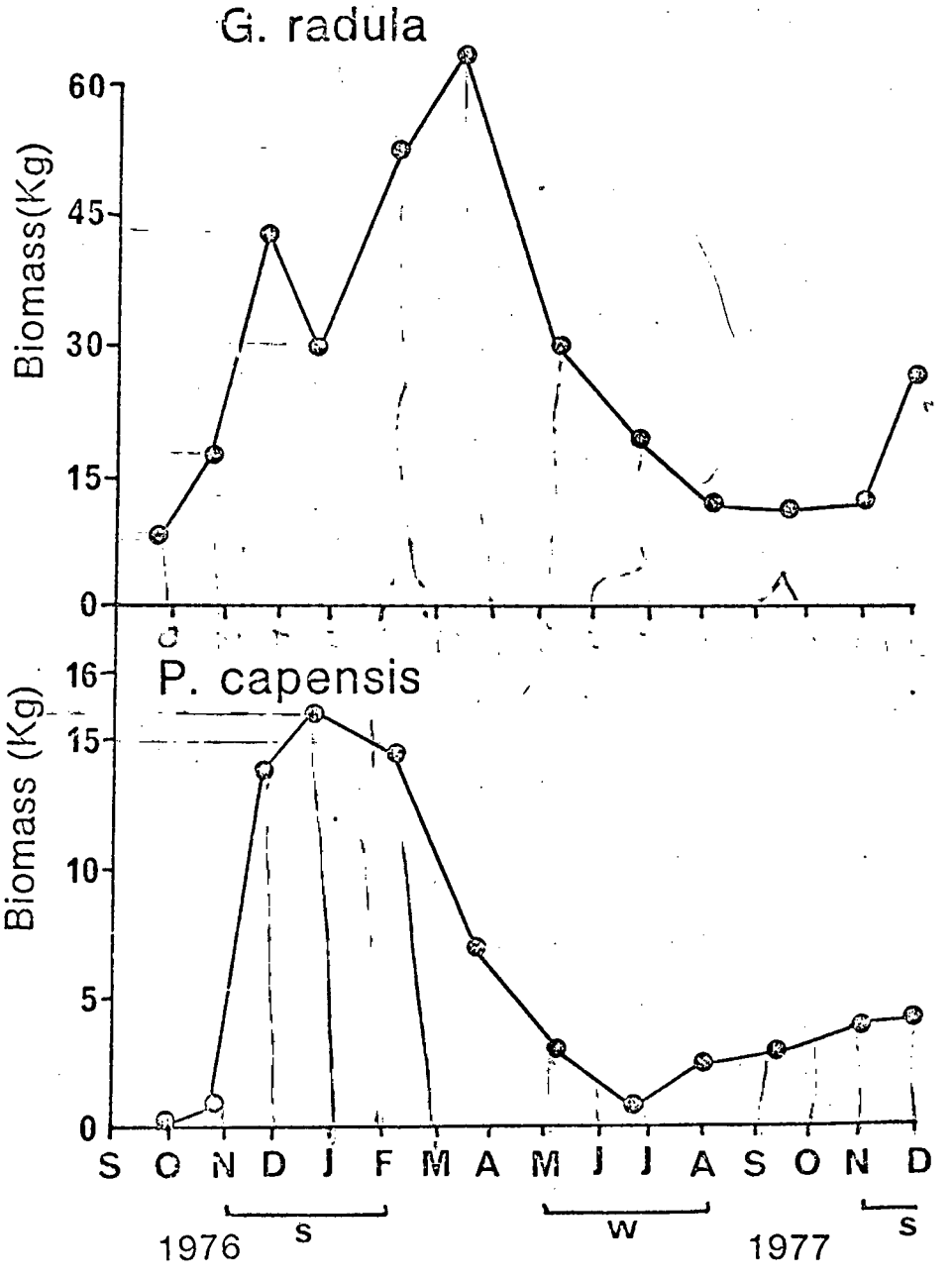

G. radula
Biomass(Kg)
60
45
30
15
0
P. capensis
Biomass (Kg)
16
15
10
5
0
S O N D J F M A M J J A S O N D
1976
s
w
1977
s

Fig. 2.1 (Cont'd)

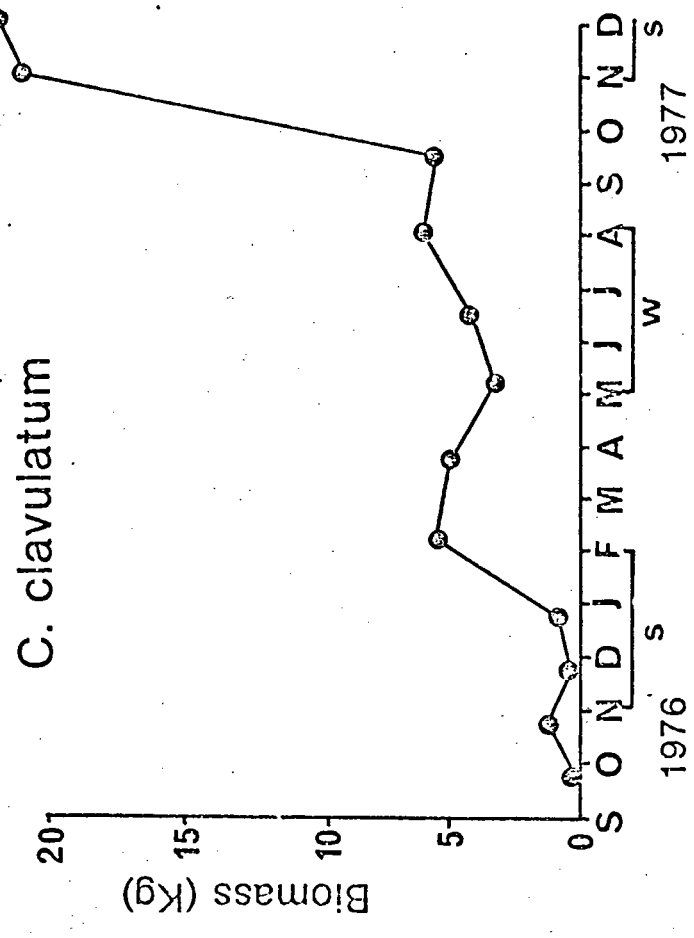

C. clavulatum
Biomass (Kg)
20
15
10
5
0
S O N D J F M A M J J A S O N D
1976
1977
S
W
S

Fig. 2.1 (Cont'd).

(b) Non-seasonal variations

In addition to these seasonal patterns of biomass there is evidence of longer term, non-seasonal changes. During the period of sampling new settlements of P. capensis and Ulva sp. occurred.

After reaching peak values in March 1977 the percentage cover and biomass of P. capensis declined dramatically and then stabilized at low values for the duration of the sampling period. Checks in 1978 revealed that P. capensis declined in biomass and by February 1979 it had completely disappeared from the beach.

The remaining species revealed considerable differences in maximum biomass between 1976 and 1977. Values were higher during the first year for Arthrocardia sp., and the dominant species P. cloiophylla, P. capensis, G. pristoides and G. radula. Higher values occurred during the second year in the case of Ulva sp. and the sub-dominants C. clavulatum, C. erinaceum and G. stiriata. These longer term patterns were superimposed on yearly periods of high biomass. Irregularity of periods of very high biomass was highlighted by G. radula. Despite a massive bloom in February 1977 G. radula was present at much lower biomass in February 1978. In February 1979 coverage was only 40 - 45 %, greatly below the 100 % attained in 1977. Although no measure was taken, biomass $.m^{-2}$ was obviously also very much lower.

The five dominant species described all reached peak biomass during periods of higher low tides (see fig. 2.3) while the sub-dominants peaked before or after this period. Different conditions of tidal heights prevailed in the first and second years and may be related to the different levels of biomass attained in these two years (see below).

2. Physical factors.

Figs. 2.2, 2.3 show seasonal variations in sunlight, sea temperature and mean low-tide heights (see below) for the years 1976-1978. Sunlight values were obtained for D.F. Malan airport (approximately 30 km from study site) from the Department of Transport. They are given as global radiation (ie. direct and reflected radiation) in cal $.m^{-2}$ $.day^{-1}$.

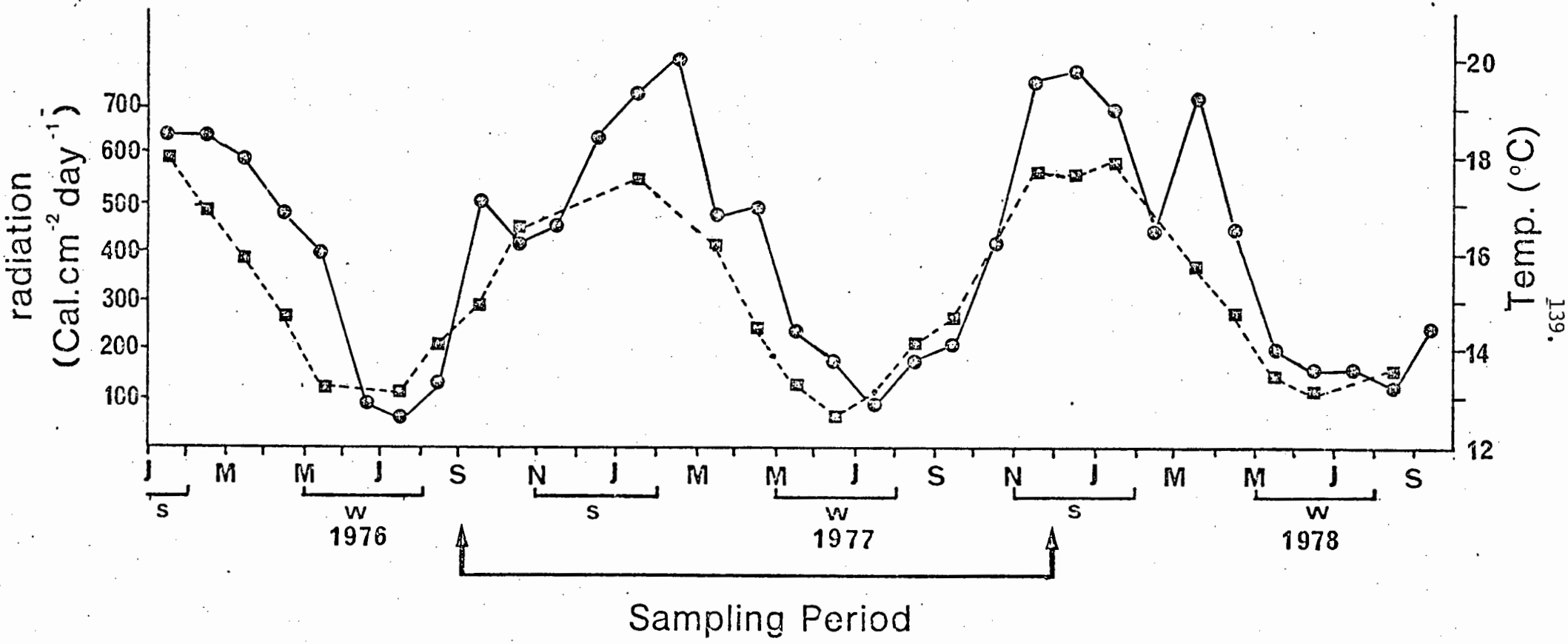


Fig. 2.2 Variations in monthly means of daily global radiation and sea temperature over a 3 year period at D.F. Malan airport and Muizenberg respectively. Data kindly provided by Department of Transport and the Maritime Weather Office, Silvermine.
(● = Temp., ■ = radiation).

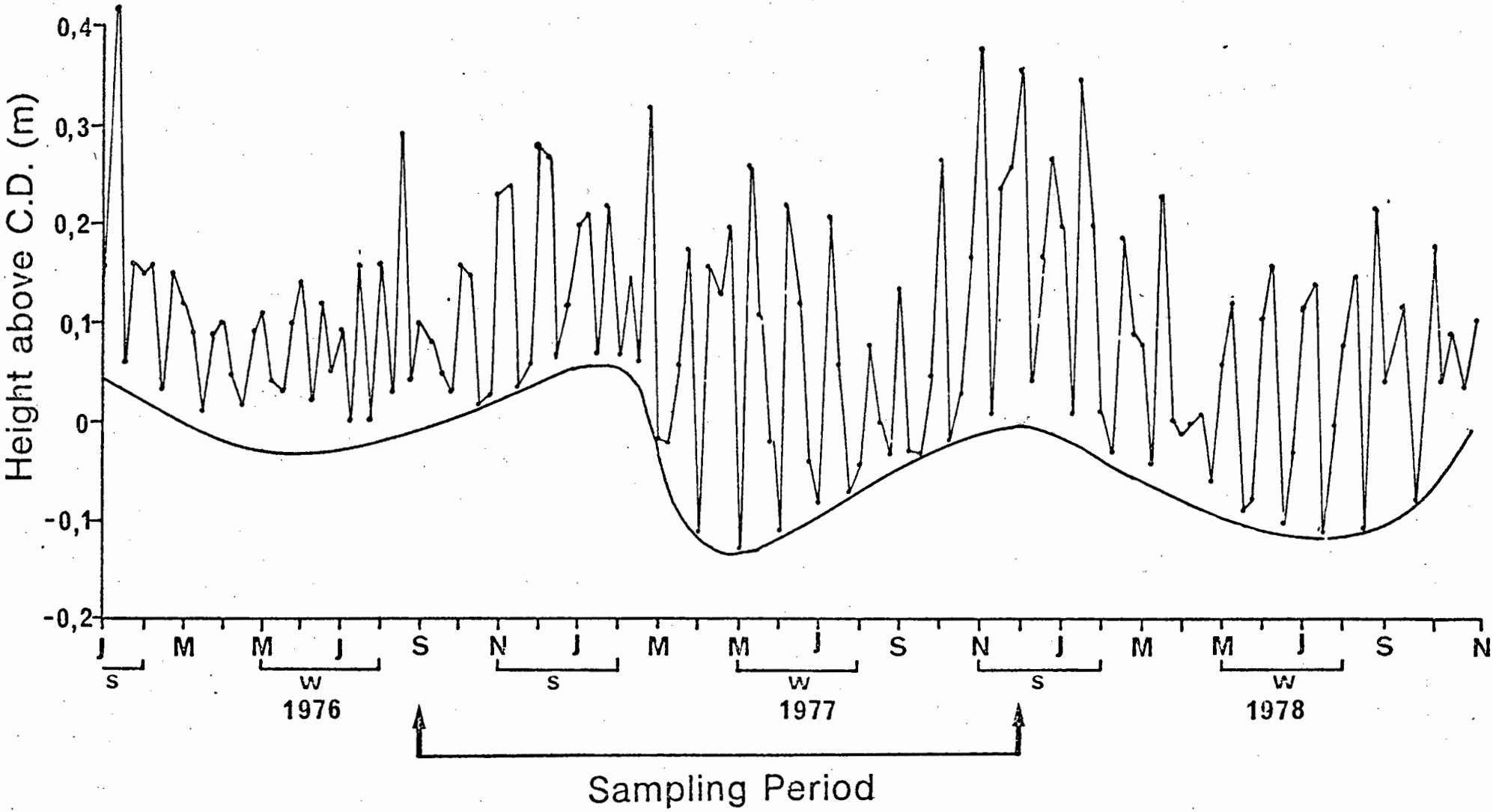


Fig. 2.3 Variations in the predicted height of the lowest diurnal tide of each week over a 3 year period. Data derived for Simons Bay (approx. 7 km from study site) from the South African tide tables (Anon., 1976, 1977, 1978).

Sea temperature values were obtained from the Maritime Weather Office. They indicate surface temperature at 0900 hours at Muizenberg (2 km from study site) and are given as monthly means of daily temperature readings. Seasonal changes in tidal conditions have been observed by Lawson (1957) and Mshigeni (1977). These were examined by plotting the height of the lowest diurnal tide (ie. between 6.00 a.m. and 6.00 p.m.) for each week. As can be seen in fig. 2.3 low tides tend to be higher in summer and lower in autumn/winter. These data are based on predicted tide levels (Anon., 1976, 1977, 1978) but the predominantly onshore south-east winds of summer and offshore north-west winds of winter may be expected to augment these predicted effects. Two further points arise from this figure. Firstly, the periodicity of this effect is less regular than that of temperature and sunlight (lowest tides occur in June-July 1976; April-May 1977; and August-September 1978). Secondly, the low tides for 1976 (covering the first four months of sampling) were unusually high, no tides below 0 m being predicted for this entire year. A completely different regime of low tides thus prevailed in 1976 and 1977, presumably due to variations in the interactions of major tide influencing factors (Shillington, pers. com., 1979).

3. Cross-correlations

In order to examine both immediate and delayed correlations between biomass and abiotic conditions correlations were performed for lag periods of 0 - 6 each lag period being six weeks (ie. lag periods of 0 - 8,5 months). Biomass is thus correlated with abiotic conditions which prevailed 0 - 8,5 months before collection. The results of these analyses are given in figs. 2.4a, b and summarized in Table 2.1.

(a) Correlation between abiotic factors:

All three factors are closely correlated. Changes in the height of low tides precede changes in light intensity slightly which in turn precede changes in sea temperature. Thus tide and light changes correlate best at lag 0 as do changes in mean monthly light radiation and mean monthly sea temperature. Because of the slight staggering effect tidal changes precede temperature changes and best correlation occurs at lag 1. Although these changes in abiotic factors are regular, changes

TABLE 2.1 : HIGHEST CORRELATIONS BETWEEN BIOMASS AND PHYSICAL FACTORS FOR EACH SPECIES EXAMINED

(lag periods are shown in brackets and the highest correlation for each species marked with an asterisk)

	Species	Tide	Light	Temp.
1. Positive correlations	Arthrocardia sp.	*0,2391 (0)	0,1820 (0)	-0,0595 (5)
	Gelidium pristoides	*0,7295 (0)	0,4525 (0)	0,3171 (0)
	Gigartina radula	*0,7309 (2)	0,6766 (3)	0,6859 (2)
	Porphyra capensis	*0,6660 (2)	0,5240 (2)	0,5556 (2)
	Gigartina stiriata	0,2019 (0)	0,4189 (0)	*0,4502 (0)
	Pterosiphonia cloiophylla	0,4695 (5)	*0,4996 (3)	0,4278 (2)
2. Negative correlations	Centroceras clavulatum	*-0,5423 (6)	-0,4860 (5)	-0,4734 (4)
	Chaetangium erinaceum	*-0,6077 (4)	-0,5673 (3)	-0,5422 (2)
	Ulva sp.	-0,6752 (5)	*-0,6903 (4)	-0,6837 (3)

in the height of low tides do not follow a strictly twelve month cycle.

(b) Correlation between biomass and abiotic factors.

A refractory period between changes in the physical environment and the response of algae as manifested by biomass changes is to be expected. Consequently biomass fluctuations frequently correlate best with changes in abiotic factors after a lag period of several weeks or months. Doty (1971b) found that the correlation between algal biomass and abiotic factors decreased as lag period decreased ie. biomass was more closely correlated with abiotic conditions prevailing some weeks before collection than with conditions during the collection period. In the present study best correlations for many species also occurred with a lag period greater than zero. All three of the factors examined, and presumably other factors, have some influence on biomass and correlations with single factors tend to be low in some cases. Two main types of relationships are revealed:-

(i) Positive correlations (fig. 2.4a)
Four of the dominant species showed positive correlations between biomass and abiotic factors. Best correlations with all three factors occur at 0-4,5 months lag. Correlation was highest with tidal height for Gelidium pristoides, Porphyra capensis and Gigartina radula (Table 2.1). For G. pristoides this occurred at lag 0 indicating that current tidal condition is the dominating abiotic factor influencing biomass. For P. capensis and G. radula biomass changes follow changes in the height of low tides after a 3,5 months lag period (ie. lag 2). Biomass of Pterosiphonia cloiophylla correlates best with light intensity, with a 4,5 month lag period. Positive correlation is exemplified in fig. 2.5a which shows a regression of G. pristoides biomass against concurrent height of low tides (ie. tidal height at lag 0). Highest correlations for the two subdominant species Arthrocardia sp. and G. stiriata are also positive but are of low values. For Arthrocardia sp. best correlation is again with tidal height. G. stiriata is the only species for which the best correlation was with temperature.

(ii) Negative correlations (fig. 2.4b)
This was shown for the two subdominant species Centroceras clavulatum and Chaetangium erinaceum which are present at quite low biomass throughout the year, and for Ulva sp. Negative correlation indicates

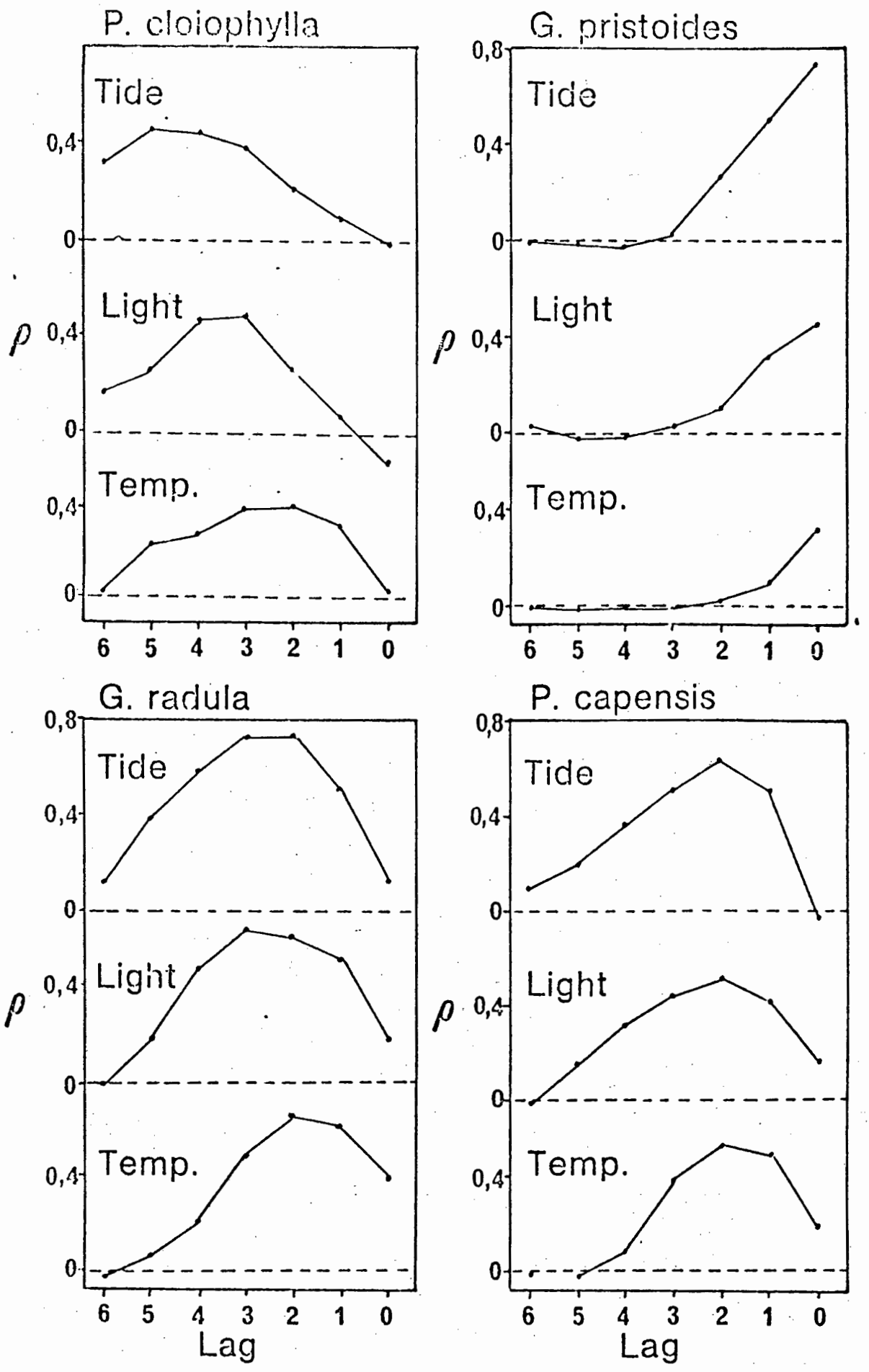


Fig. 2.4 Results of cross-correlation analyses between algal biomass and physical factors. Analyses performed for lag periods of 0-6 x 6 weeks. A : Species showing positive correlations.

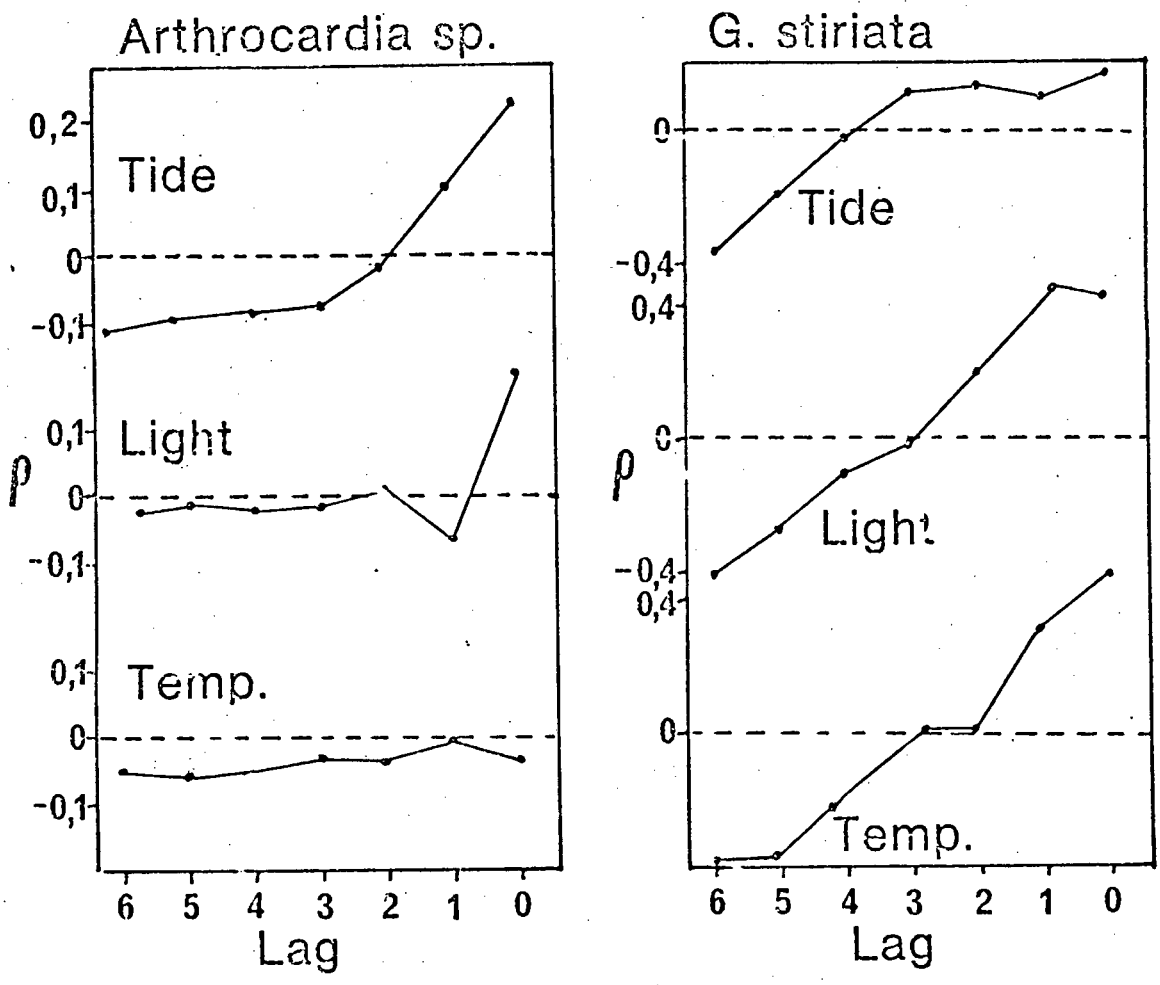


Fig. 2.4A (Cont'd).

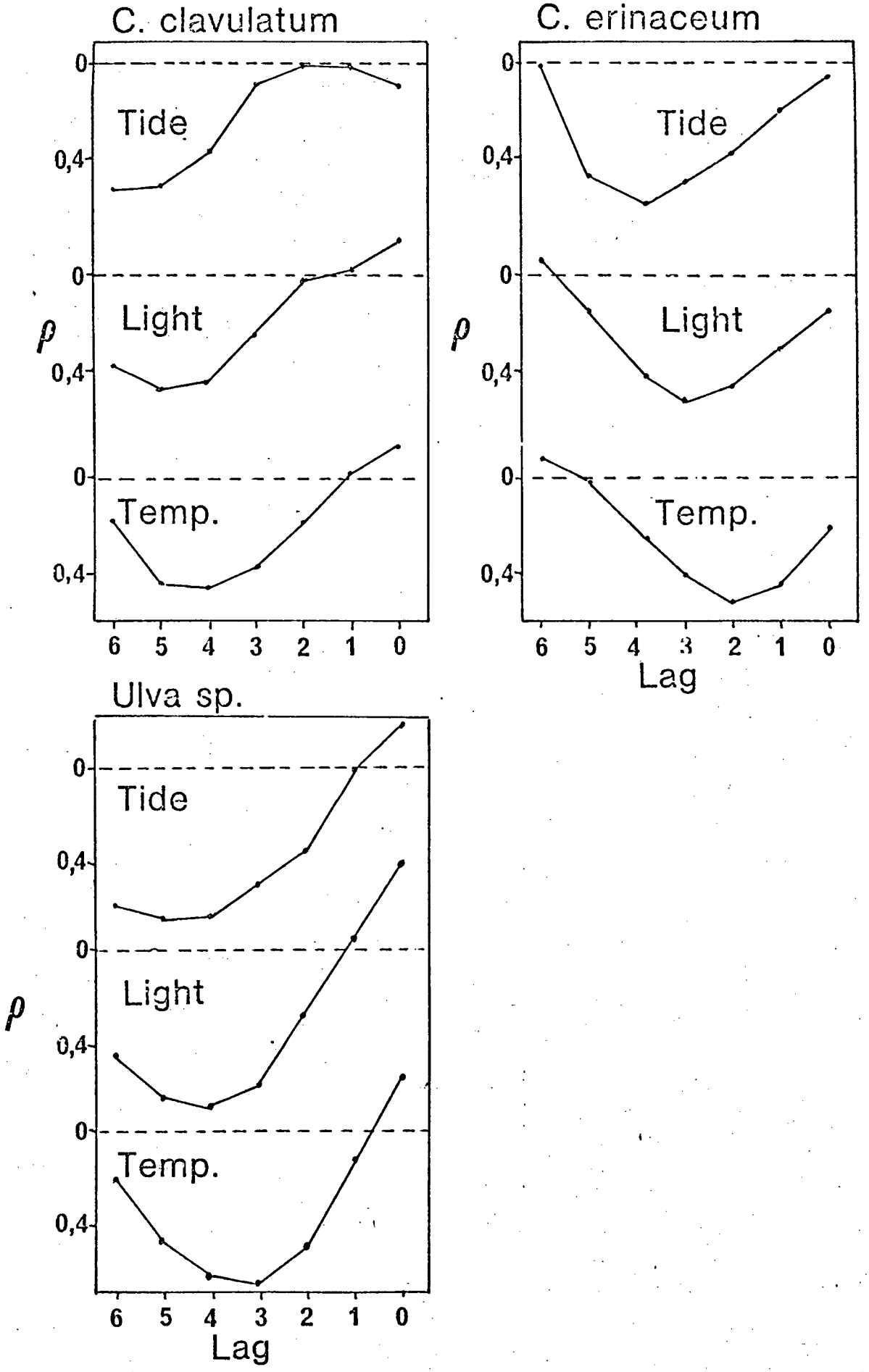
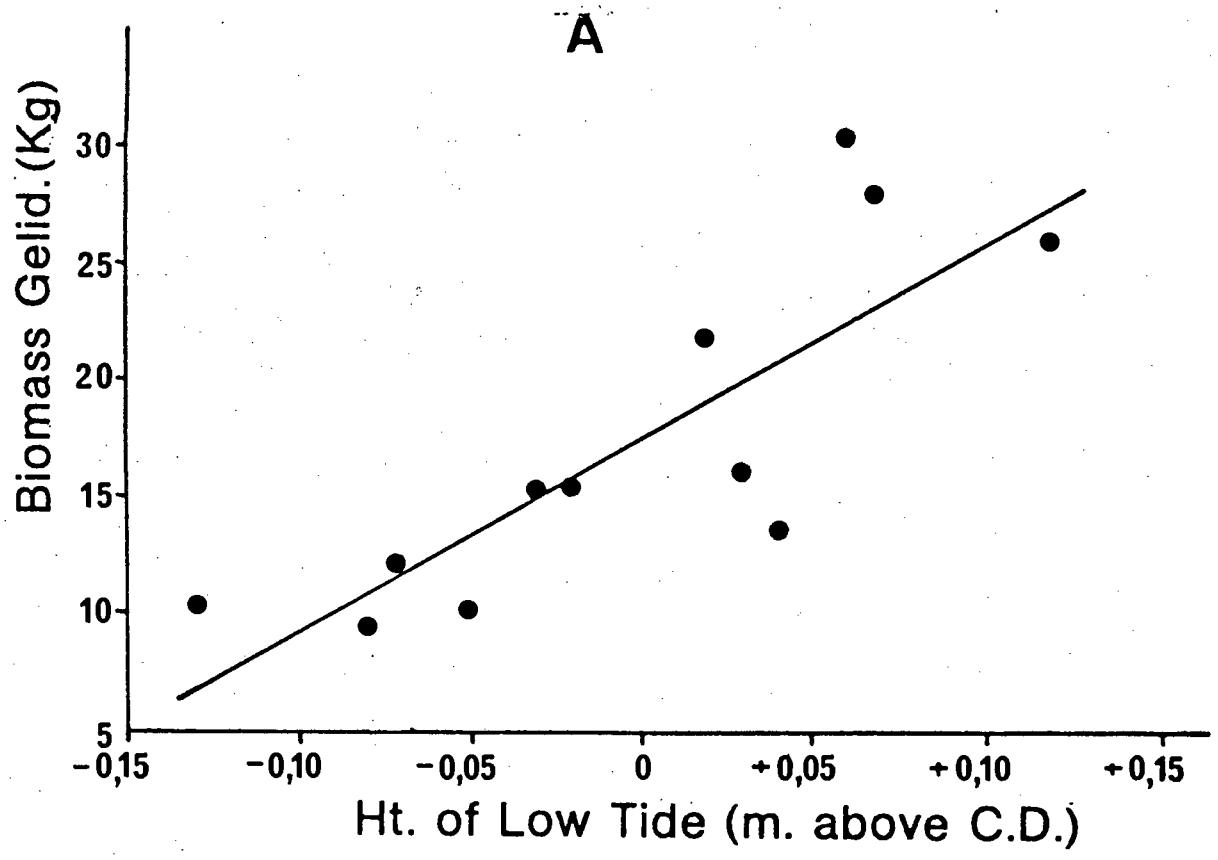


Fig. 2.4B : Species showing negative correlations.

Fig. 2.5 A The relationship between biomass of Gelidium pristoides and the height of lowest diurnal tides.
(Positive correlation : r = 0,79).

B The relationship between biomass of Ulva sp. and mean daily radiation. Biomass values were plotted against radiation values from four sampling periods earlier i.e. lag 4.
(Negative correlation : r = 0,87)
Points denoted O indicate lowered biomass due to competition when biomass of G. pristoides was high (Sept.-Nov. 1976). These points were omitted from the regression calculation.


A
Biomass Gelid.(Kg)
30
25
20
15
10
5
-0,15
-0,10
-0,05
0
+0,05
+0,10
+0,15
Ht. of Low Tide (m. above C.D.)

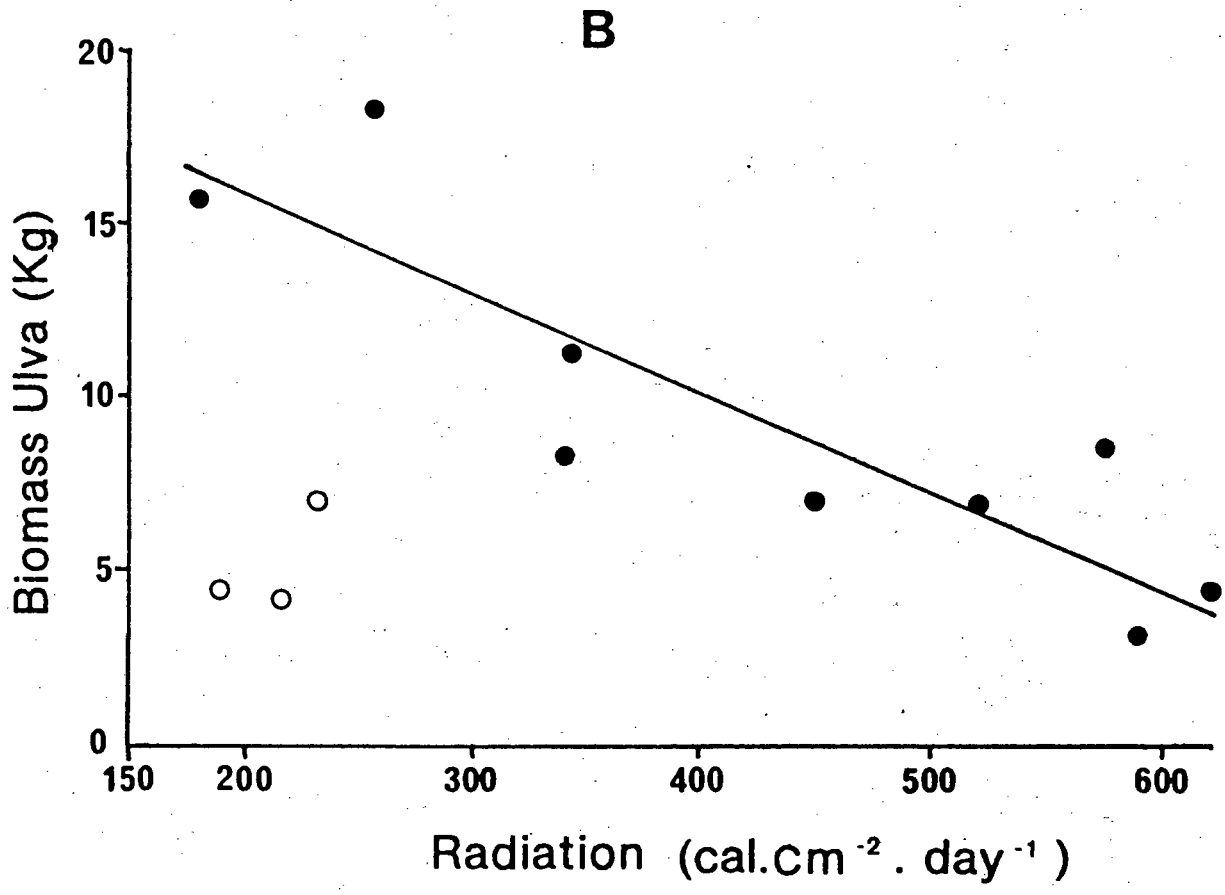

B
Biomass Ulva (Kg)
20
15
10
5
0
150
200
300
400
500
600
Radiation (cal.Cm -2 . day -1)

Fig. 2.5

that increase in abiotic factors correlates with a decrease in biomass. Longer lag periods are involved and absolute correlation values are, with the exception of Ulva sp., lower.

For C. erinaceum and C. clavulatum height of low tides again appears to be the dominating factor. Biomass decreases in response to increase in the height of low tides after a lag of 6 and 9 months respectively. Ulva sp. correlates best with light intensity with a lag of 6 months. Fig. 2.5B gives an example of negative correlation, showing a regression of Ulva sp. biomass against light intensity at lag 4 (ie. light intensity 6 months prior to each biomass collection).

Thus biomass fluctuations may be positively or negatively correlated with the height of low tides, temperature or light intensity. Of the five dominant species, G. radula, G. pristoides and P. capensis correlate most closely with tidal height. Although Ulva sp. and P. cloiophylla correlate best with light they both also show a high correlation with tide effects. All of these species tend to reach peak biomass during periods of higher low tides, as described. All the dominants except Ulva sp. showed positive correlation with abiotic factors. If the absolute correlation value is considered, ie. the sign is ignored, a t-test indicates that dominant species show a significantly higher correlation than sub-dominants ($P < 0,05$), with the exception of P. cloiophylla. This indicates that biomass of dominant species is influenced to a greater degree by abiotic factors than biomass of subdominant species, although this influence may have a positive or a negative effect on biomass. Correlation values suggest that the most important of these factors is the height of low tides. None of the subdominant species shows a completely positive correlation with the three factors considered. Biomass of subdominants is generally negatively correlated with abiotic factors although best correlation was positive for two species. However the lower correlation values indicate that other factors are important in determining biomass values.

4. Zonation

Vertical distribution and biomass in each zone are given for each species for the duration of the sampling period in figs. 2.6 A-G. Three forms of change in zonational patterns were observed during 15 months of sampling.

(a) Extension of range.

This was the most common form, occurring in all the mid-tidal species and, during brief periods, in P. cloiophylla (fig. 2.6B). It entailed an up or downshore extension from the main population area into adjacent zones where the particular species in question did not previously occur. Summer extensions of range lasting 4-5 months were observed for C. erinaceum, G. stiriata and G. radula while longer term summer extensions of 6-7 months occurred in G. pristoides and Ulva sp. (figs. 2.6A-F). A brief seasonal upward extension lasting 1-2 months during each spring occurred in P. cloiophylla.

G. radula and C. clavulatum (figs. 2.6F, G) were the only species which showed a downshore extension of range. G. radula extended both up and downshore during late spring and summer, receding during winter and extending again the following spring. C. clavulatum was the only species which extended its range during winter/spring. During June and September its range extended both up and downshore and receded again for the rest of the year.

(b) Zonation changes

These entailed a vertical shift of the zone of distribution of a species. They occurred only in the mid-tidal subdominant species C. erinaceum and G. stiriata. C. erinaceum (fig. 2.6C) was found only in zone 7 in spring and early summer (September-November 1976). From mid-summer through winter however it was found only farther upshore in zones 8 and 9 moving downshore again the following spring (September 1977). This results in an upshore shift of distribution from late summer through the winter. G. stiriata (fig. 2.6A) occurred exclusively in zone 7 during mid-summer (December- February) but from autumn to spring (March-September) it was found only farther

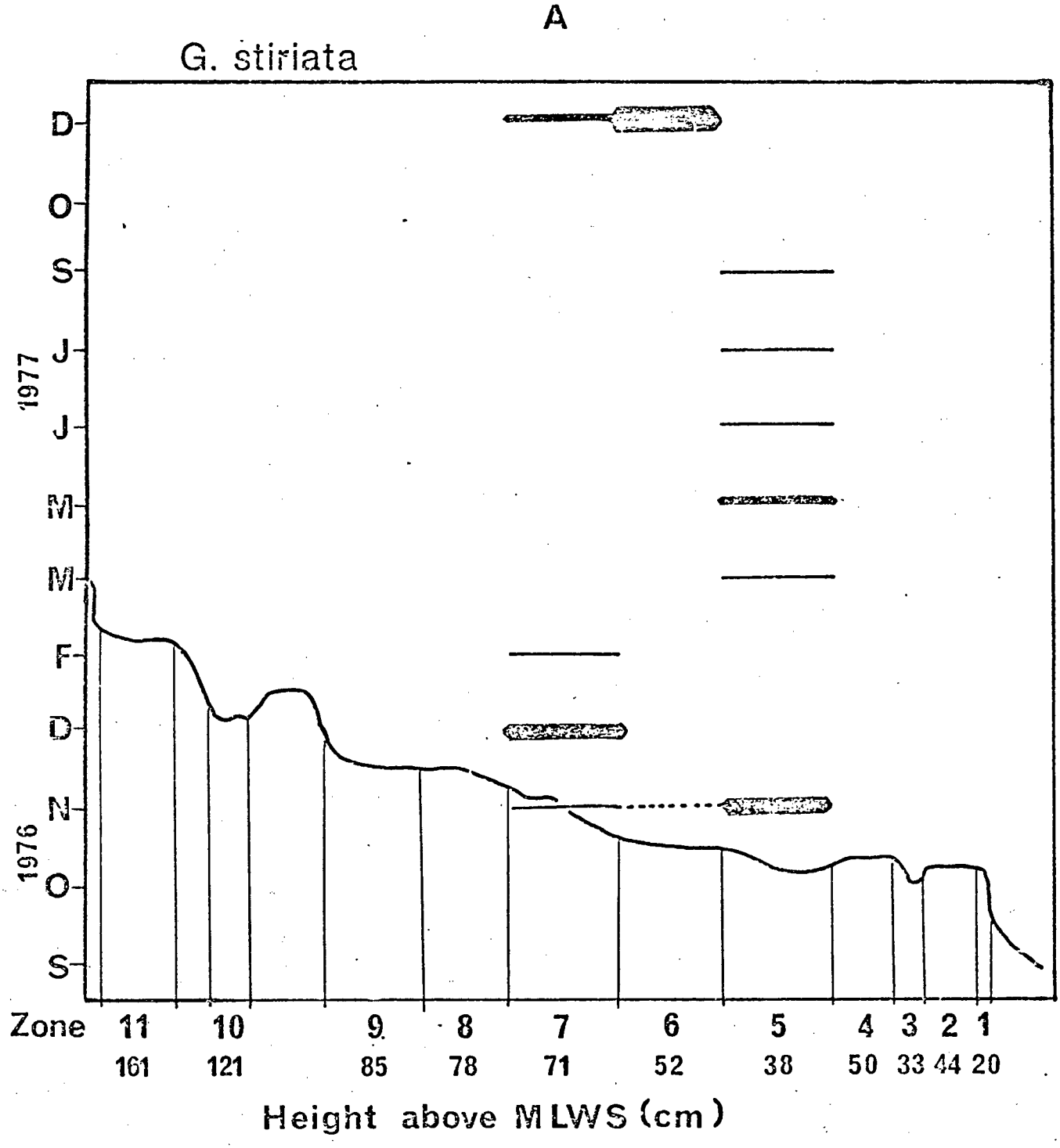


Fig. 2.6 Zonation of algal biomass at Dalebrook over a period of 15 months.

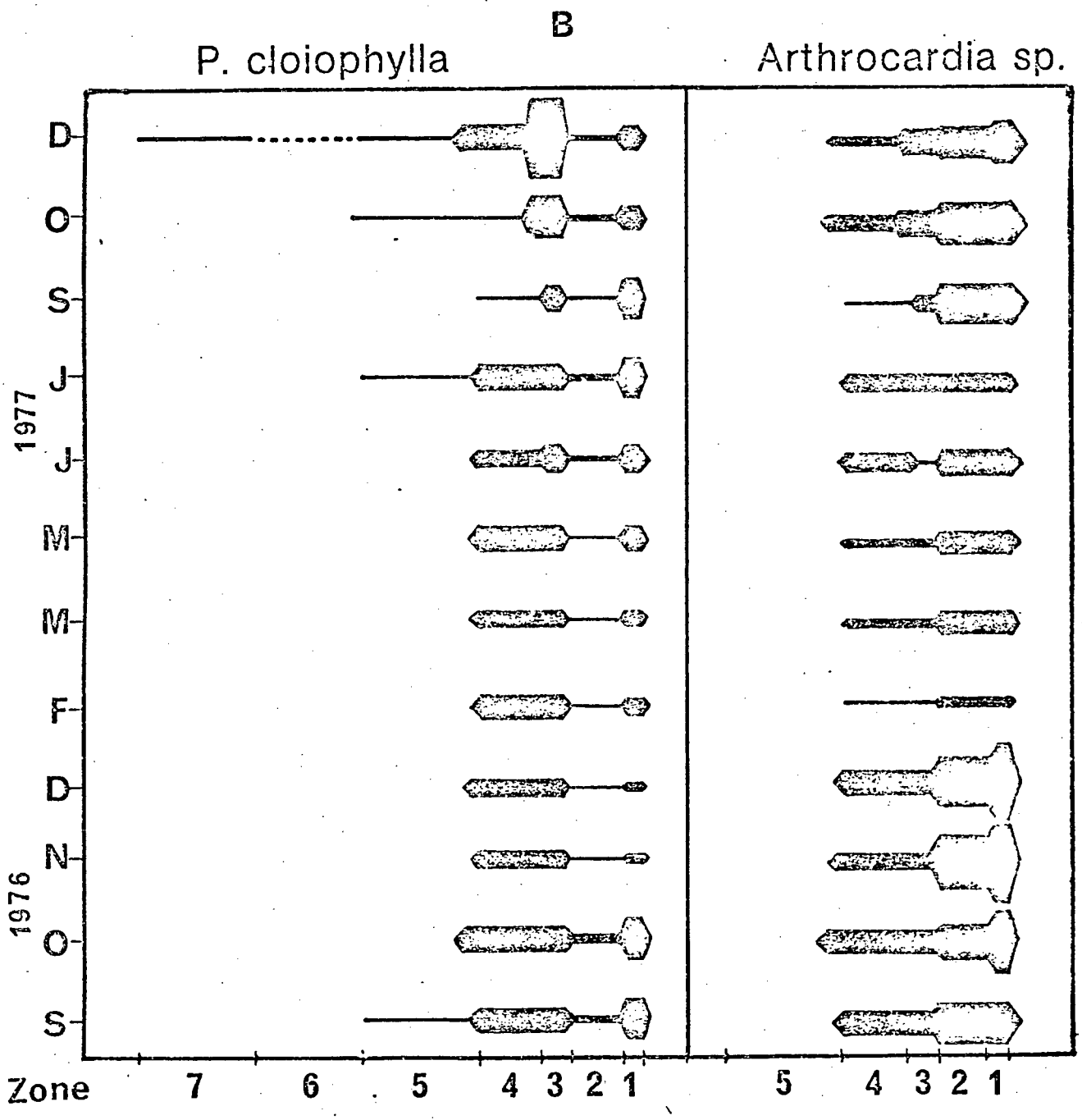

B
P. cloiophylla
Arthrocardia sp.
D
O
S
J
J
M
M
F
D
N
O
S
1977
1976
Zone
7
6
5
4
3
2
1
5
4
3
2
1

Fig. 2.6 (cont'd)

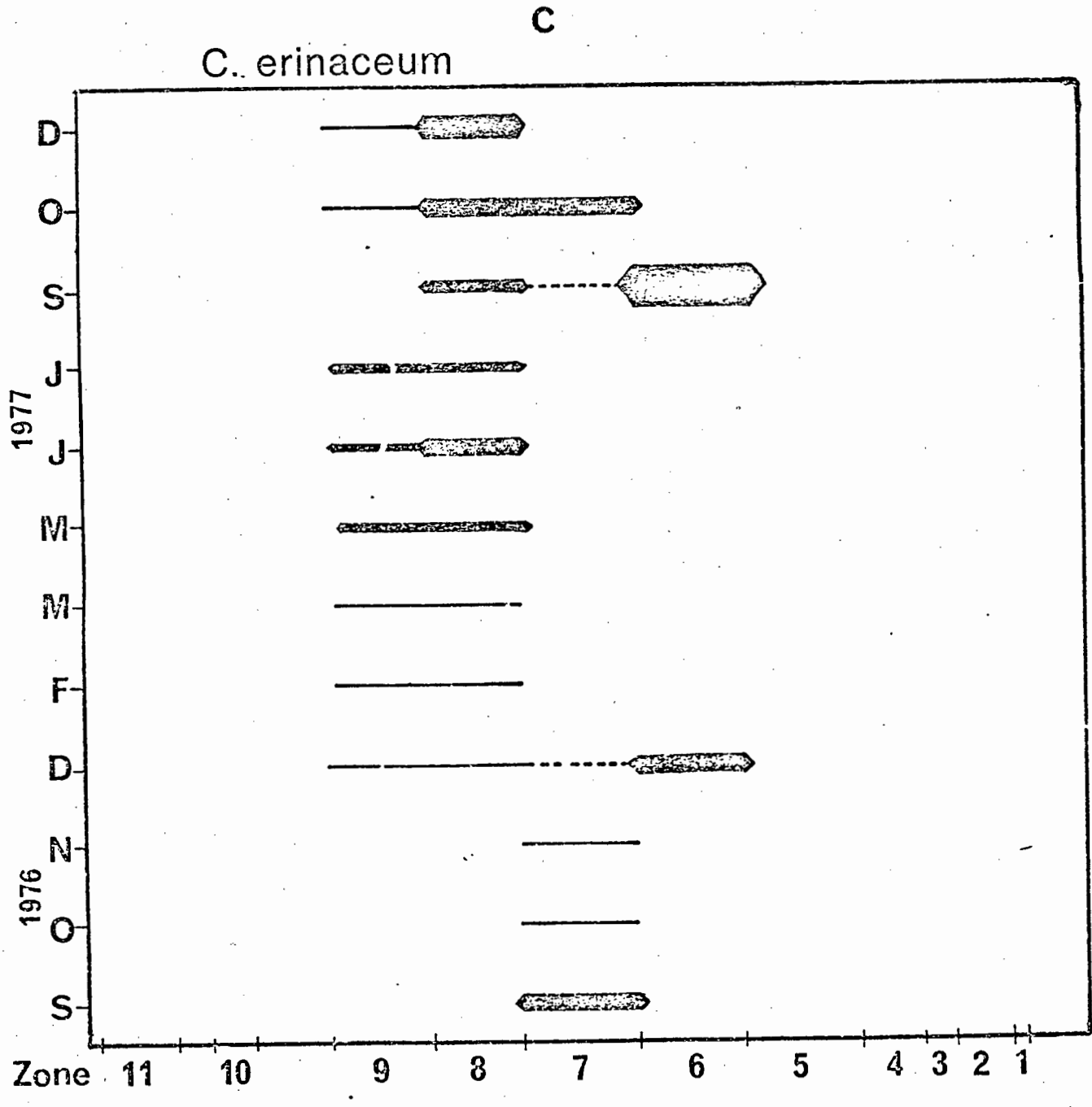


Fig. 2.6 (cont'd)

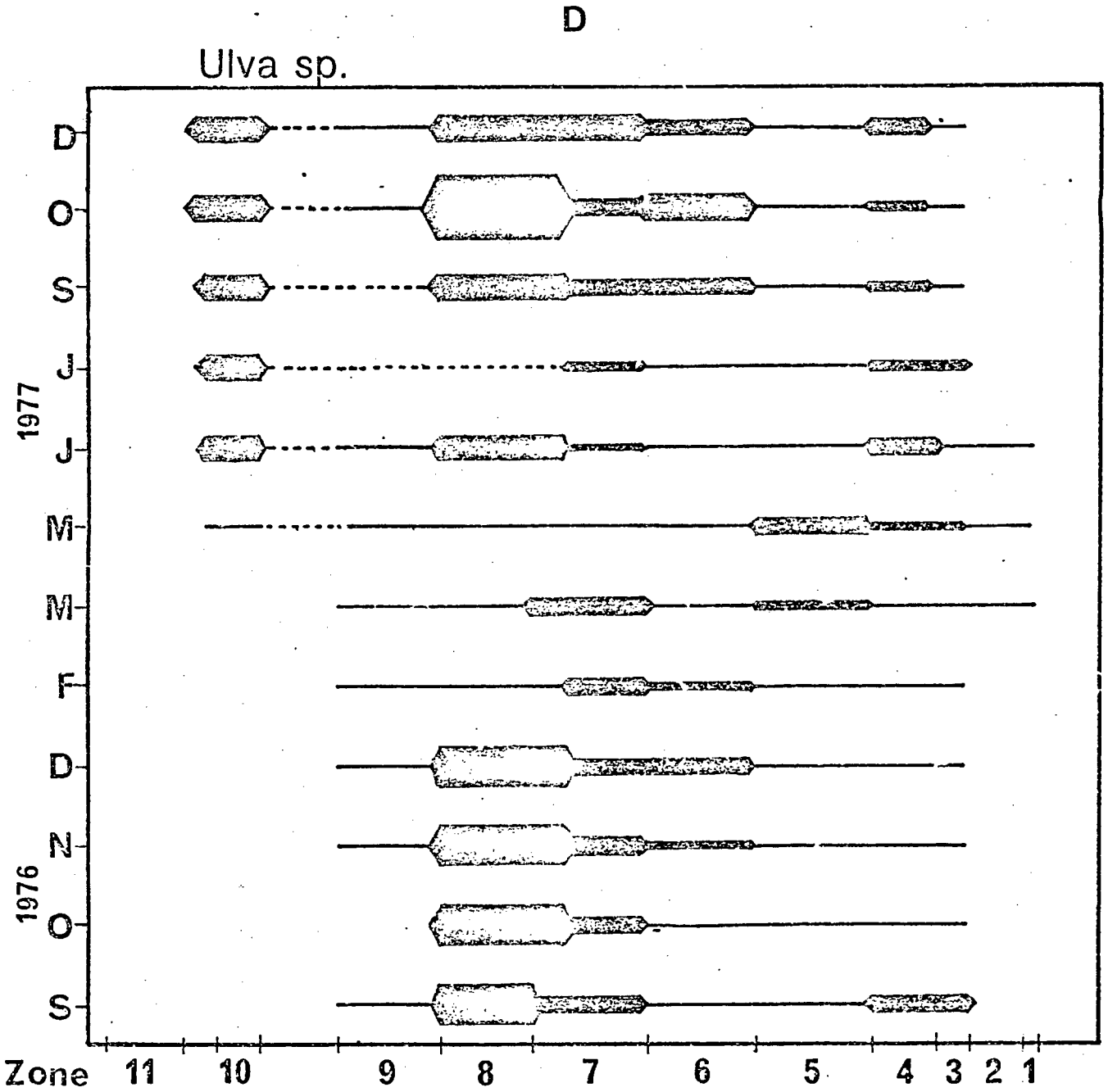


Fig. 2.6 (cont'd)

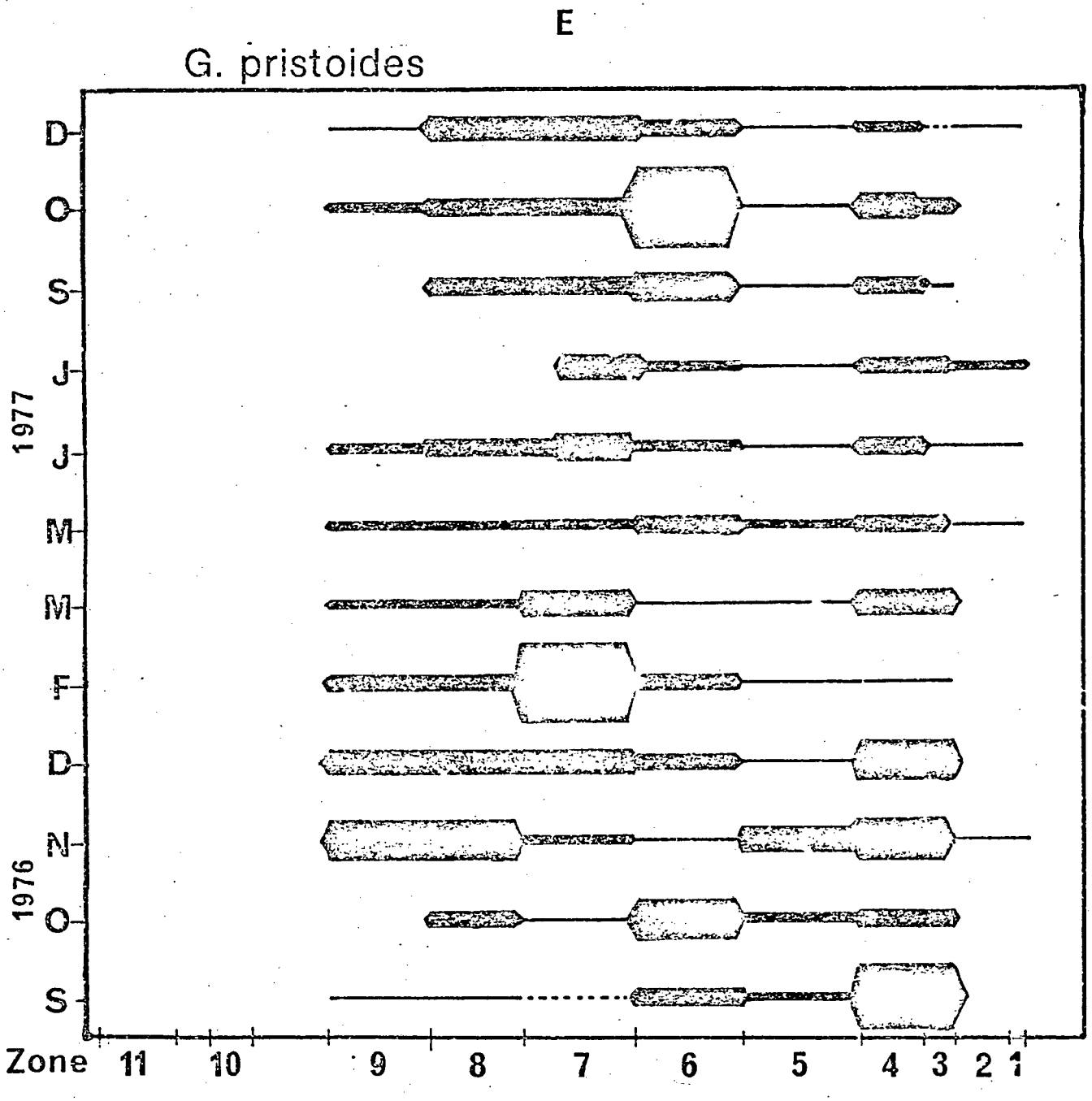


Fig. 2.6 (cont'd)

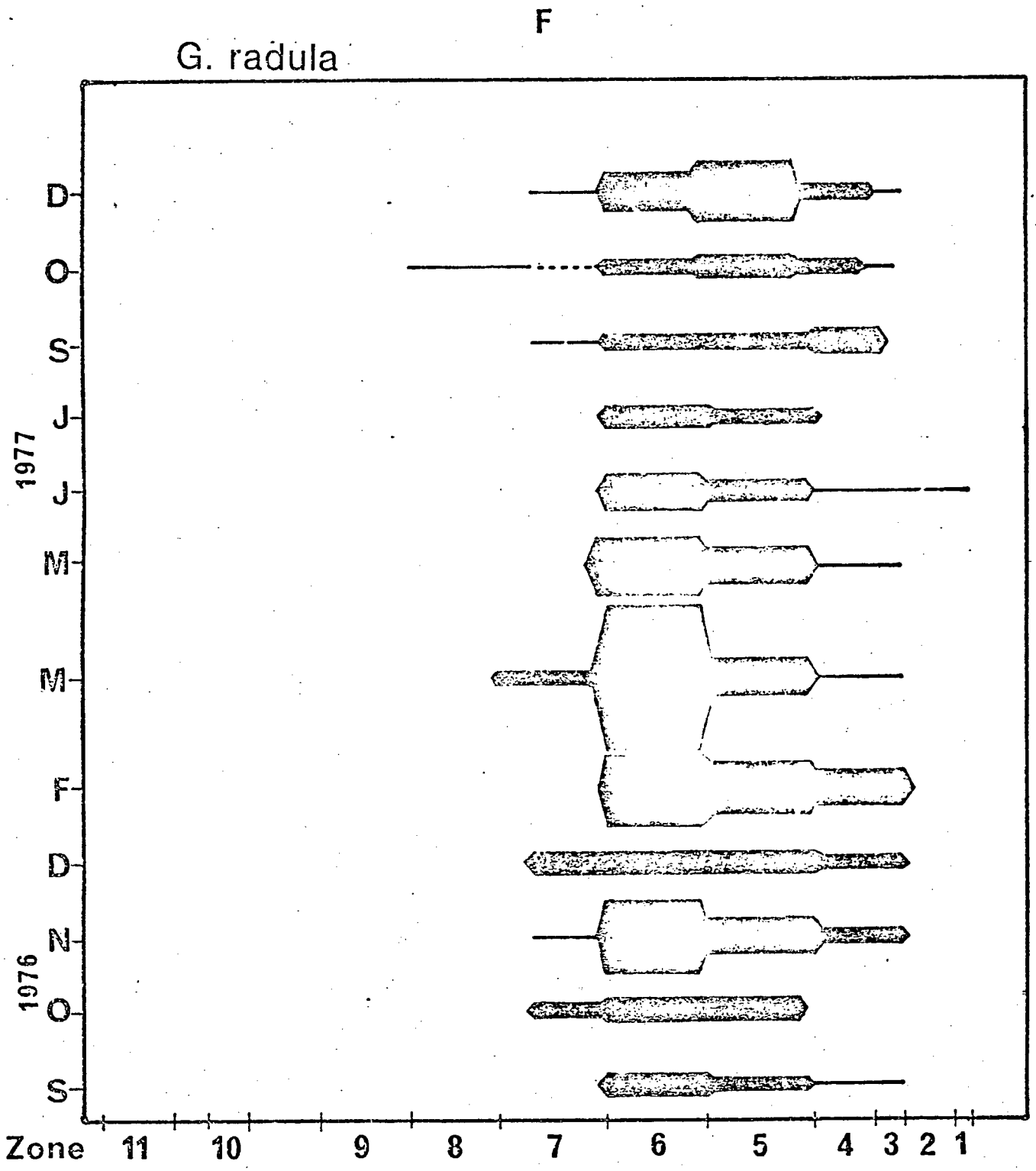


Fig. 2.6 (cont'd)

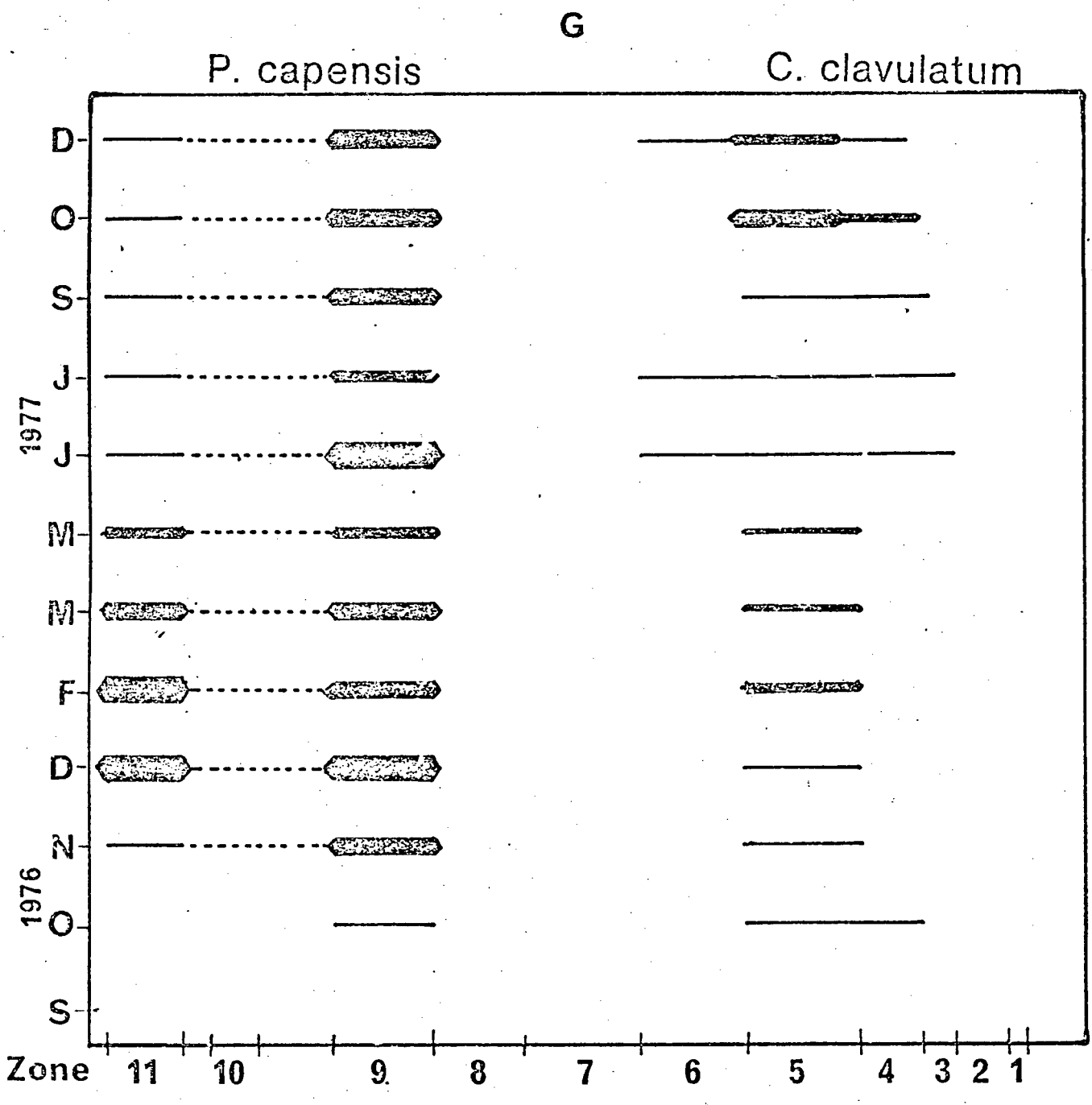

G
P. capensis
C. clavulatum
D
O
S
J
J
M
M
F
D
N
O
S
1977
1976
Zone
11
10
9
8
7
6
5
4
3
2
1

Fig. 2.6 (cont'd)

downshore in zone 5. Thus distributional range was higher upshore during the summer, an effect similar to the summer upshore extensions of other species.

(c) Changes in the zone of maximum biomass.
These were in some cases very marked and occurred when a species occupied a number of zones, usually adjacent to each other. It was found that the area of maximum density for particular species shifted to different zones at different times of the year. P. cloiophylla was the only species for which the area of maximum density shifted upshore during spring or summer. Downshore shifts during spring/summer occurred for G. radula, Ulva sp. and G. pristoides. In the case of Arthrocardia sp. (fig. 2.6B) although maximum density was found at zone 2 throughout the year similar levels of density occurred in zone 4 during winter (June, July).

In addition to these seasonal zonational changes long-term non-seasonal changes were observed for P. capensis and Ulva sp. as described. P. capensis first appeared in zone 9 in October 1976 and in zone 11 in November 1976 (fig. 2.6G). A new settlement of Ulva sp. higher up the shore than the existing population occurred in zone 10 in May 1977 (fig. 2.6D).

5. Ash content

Percentage ash content varied considerably during the course of sampling (fig. 2.7). Ash content was lowest during autumn or winter for almost all species. This is in contrast to the findings of Wort (1955) but agrees with those of Black (1950), MacPherson and Young (1952) and Himmelman and Carefoot (1975). Two main patterns are evident.

(a) Values maximal in spring (October) and decline gradually through summer to a minimum in winter. This pattern was found for G. pristoides, P. capensis, Ulva sp. and C. erinaceum. In the case of Arthrocardia sp. the pattern was modified in that minimum values occurred in early autumn and ash content rose again through late autumn and winter, to peak in spring.

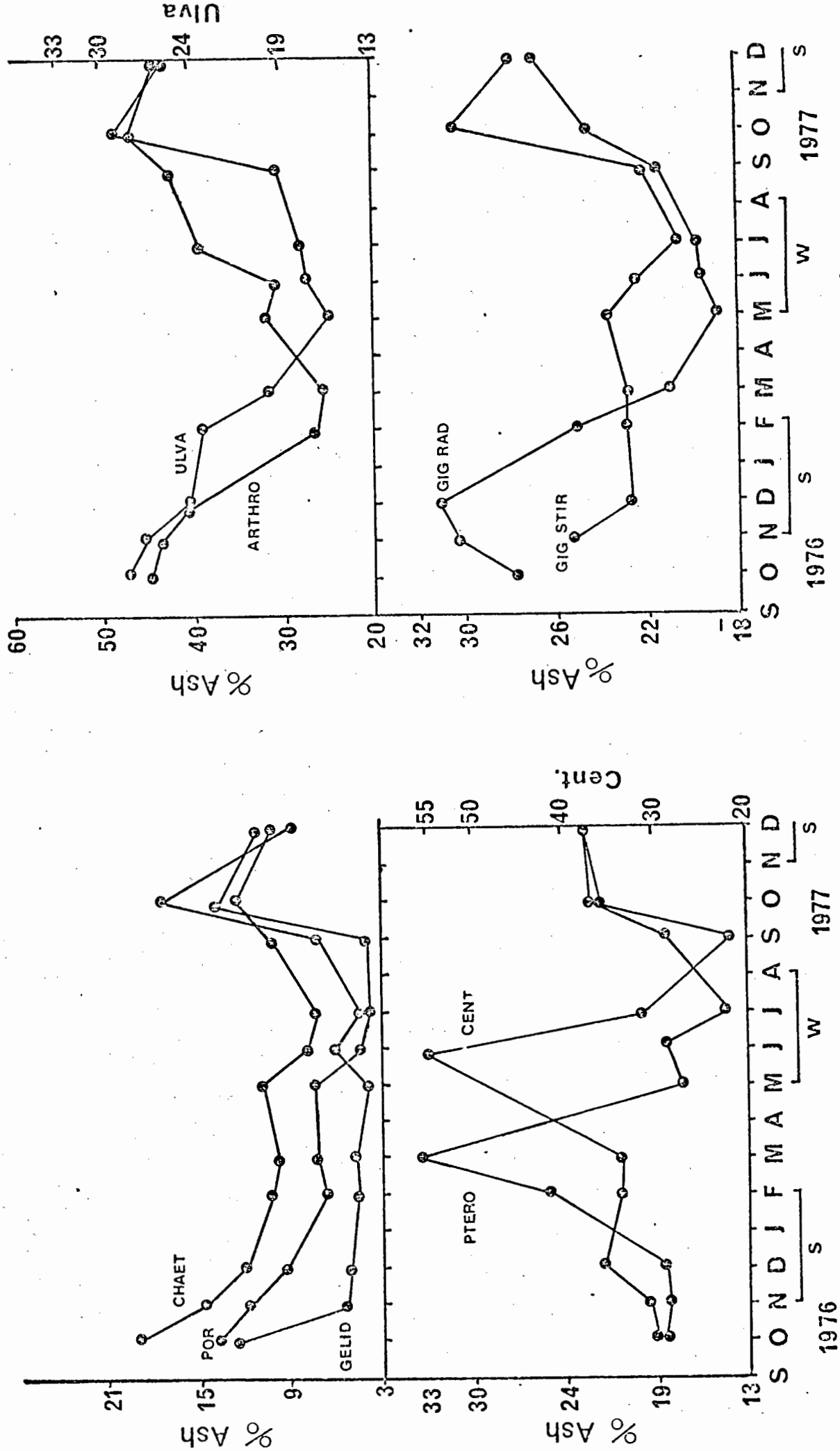


Fig. 2.7 Percentage ash content of dried algal samples over a period of 15 months.

(b.) Peak values occur slightly later, in summer. Ash content then declines through autumn, again to minimal values in winter. This was found for P. cloiophylla (with peak values in early autumn) and for G. radula. G. stiriata shows a similar but less clear pattern.

The absence of a clear pattern for C. clavulatum is probably due to the difficulty in obtaining a perfectly sand free sample for this filamentous species. If the very high value for June is discounted as being due to this,then ash content again seems to peak in October/ December.

6. Calorific values

The calorific values derived are very similar to those obtained by Beckley (1977) in June for some of the same species on St. Croix Island near Port Elizabeth.

Ash free calorific values are given in fig. 2.8 and were found to fluctuate considerably during the year. For most species a seasonal pattern is apparent.

Arthrocardia sp.: maximum values in mid-summer, declining through autumn and winter to minimum values in early spring and increasing again at the start of the next summer.

Pterosiphonia cloiophylla: values increase from a minimum in early summer to maximum values at the end of summer/autumn. A brief decline in early winter is followed by a winter/spring increase. Values then decrease to a minimum again in early summer.

Centroceras clavulatum: minimum values occur in late summer/autumn and increase to maximum values in spring, declining again towards early summer. The high value for June is due to the probably erroneously high ash content for that month (see above).

Chaetangium erinaceum: an irregular fluctuation is apparent for this species but values appear to be maximal in mid-summer (December) during both years.

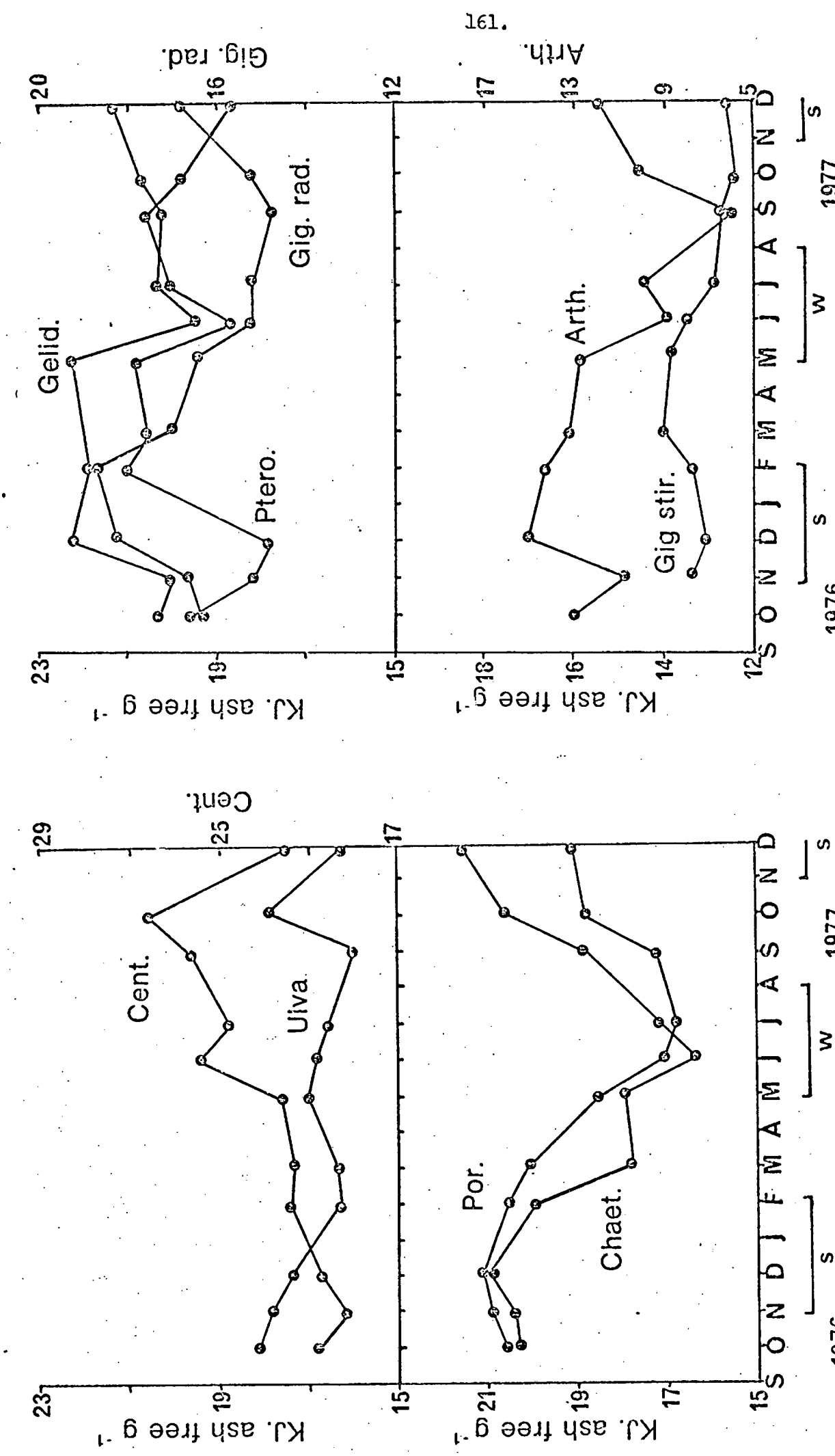


Fig. 2.8 Variations in calorific content of algae over a period of 15 months, based on ash free dry weights.

DISCUSSION

Biomass changes

The results of the present study confirm those of Isaac (1937) in that seasonal changes did not result in any algal zone disappearing, nor were any of the dominant species of any zone replaced by other species during part of the year. Although the general character of the vegetation remains constant throughout the year the beach as a whole is however dominated, in terms of biomass, by different species at different times (fig. 2.1).

Isaac (1937) recognised more luxuriant growth at different seasons and during this study marked changes in standing crop were exhibited by all species. Most species attained maximum biomass in spring or summer as has been found by previous workers (eg. Lawson, 1957; Underwood, 1973; Dawes, Mathieson and Cheney, 1974; Mathieson et al, 1976; Mshigeni, 1977; Brinkhuis, 1977a; Druehl and Hsiao, 1977 and Santelices, 1977). Although the levels of biomass were considerably different in 1976 and 1977 in almost all cases, most species showed regular peaks of biomass in the same month each year.

The case of Porphyra capensis is interesting as it attained maximum biomass in early autumn and then declined while previous workers found that it flourishes best during spring or winter (Bokenham and Stephenson, 1938; Isaac, 1938). Beckley (1977) found that plants of P. capensis which settled in June (winter) reached maximum size six months later. The settlement observed at Dalebrook in October reached maximum biomass six months later in March. Growth patterns of this species and the time of settlement may thus account for an autumn peak of standing crop. Disappearance of the Porphyra zone however was a long term effect rather than a seasonal one and occurred only after approximately two years from the time of initial settlement (p. 138).

In order to understand seasonal variations in biomass we must examine the biotic and abiotic factors which may be expected to have an important influence.

Biotic factors

Two forms of biotic interactions are important in influencing algal standing crop; grazing and competition.

1. Grazing

Work by Dayton (1975) suggests that interactions of predators and herbivores generally result in a balance such that grazing is not so intensive as to result in the exclusion of algal species. Menge and Sutherland (1976) also suggest that carnivore/herbivore interactions may emphasize the apparent importance of competition in primary producer associations. It has however been found by numerous workers that the effects of grazing can be severe and that algal biomass can increase dramatically in the absence of herbivores. Reduction to, or maintenance of, low levels of macrophytic algal biomass due to grazing has been demonstrated in the case of fish (Randall, 1963; John and Pople, 1973), limpets (Southward, 1969; Branch, 1971; Dayton, 1971), littorinids (Castenholz, 1961) and urchins (Dayton, 1975). Grazing may also affect the richness and diversity of algal associations. Lubchenco (1978) has shown that moderately heavy grazing of dominant algal species in pools can lead to an increase in richness by decreasing the effects of competition on sub-dominant species. She also found however that severe grazing in pools or even moderate grazing on the open beach leads to a decrease in both richness and diversity of algal communities.

Severe grazing of algae at Dalebrook appears to be limited to a few herbivores. The urchin Parechinus angulosus, although present in quite large numbers is primarily a debris feeder and although it may eliminate sporelings it is restricted to pools and gulleys. Similarly there is no evidence of large scale intertidal feeding by fish. Limpet grazing however has marked effects where limpet density is high. Although Patella cochlear feeds primarily on Lithothamnion spp. (Branch, 1974) grazing of spores leads to dramatically lowered biomass of algae and total species richness in the cochlear zone (see chapter 2). At Dalebrook a decline of algal

biomass is obvious in the lower cochlear but in the upper cochlear limpet density decreases considerably and algae become more abundant.

The fronds of Ulva sp. sometimes show signs of grazing which is probably due to the abundant herbivorous amphipod Hyale diastema, the other common species, Paramoera capensis being a scavenger (Griffiths, pers. com. 1977). As H. diastema is most abundant among clumps of Ulva sp. and Gelidium pristoides it is likely that it grazes primarily on these two species.

Large populations of the turban shells Oxystele sinensis and O. tigrina occur at Dalebrook and probably represent the most important macrophytic herbivores besides P. cochlear. There is evidence of heavy grazing of G. radula in particular which may be attributable to O. sinensis (Fielding, pers. com., 1979). It must be emphasized however that algae with a sheet-like morphology tend to show high rates of photosynthesis (Littler and Murray, 1974; Brinkhuis, 1977b) and growth of G. radula can be very rapid (up to 4,1 mg increase per month per gramme dry weight measured by Fielding (pers. com. 1979)). Biomass becomes so extremely high that, although grazing may lower actual monthly biomass, it is unlikely to influence the seasonal pattern of standing crop.

Although no attempt was made in the present study to differentiate between increase in biomass due to growth and due to new settlement it was obvious that both effects were important. It is possible therefore that grazing of algal spores by Oxystele spp. and limpets may impede seasonal increases in biomass (c.f. Jones, 1948, cited by Connell, 1972; Castenholz, 1961; Haven, 1973; Dayton, 1971). As Dayton (1975) has observed however it seems likely that rapid algal growth (eg. G. radula) swamps herbivore predation and young plants quickly grow to the size beyond which they do not suffer mortality at normal herbivore densities. Despite grazing by Oxystele spp., G. radula becomes very abundant during summer when it attains up to 100 % cover. Density at these times is so high that grazing probably has a negligible effect on biomass. The influence of grazing is probably greatest when standing crop or growth are declining or already low.

In the upper/middle balanoid (zone 9 on figure 2.6) algal biomass is always low. This is probably due to increasing physical stress higher up the shore but the effects of this are undoubtedly augmented by intensive grazing of sporlings by Oxystele variegata which is particularly abundant in this zone (see Chap. 7). For example Branch found that removal of herbivores allowed algae to appear in zones which they had not previously occupied, (unpublished data).

Two effects of grazing at Dalebrook are thus evident:

1) High limpet densities lead to low algal biomass throughout the year in the lower cochlear zone. In the upper cochlear limpet density decreases and rapid algal growth during summer overrides the effects of grazing. In zones which are marginally suitable for algae, grazing by Oxystele variegata helps to maintain low algal biomass.

2) In the remaining zones grazing pressure (mainly due to Oxystele spp. and Hyale diastema)decreases monthly values of algal biomass but is insufficient to influence seasonal patterns of biomass or cause the elimination of major species.

2. Competition.

During summer both biomass and percentage cover of algae become extremely high and interspecific competition becomes important. Competition is likely to involve three main resources: primary space (Southward, 1956; Dayton, 1971, 1975), light (John, 1969; Kain, 1969) and nutrients (c.f. Fitzgerald, 1969; Russell and Fielding, 1974: Chapman and Craigie, 1977). Inshore water at Dalebrook exhibits fairly high phosphate concentration but nitrate levels are low (Cliff, pers. com., 1979). Little seasonal variation is found in either nutrient and this may lead to increased competition when biomass is high. However, Dayton (1975) has suggested that constant water exchange in the intertidal zone prevents mineral depletion so that competition for nutrients is minimised. This is supported by the findings of Druehl and Hsiao (1977) and it seems likely that light and space are the most important factors in competition effects at Dalebrook.

In the lower cochlear zone peak biomass of Pterosiphonia cloiophylla coincides with minimum biomass of Arthrocardia sp. (fig. 2.1). This may be attributable to competition for light as the taller P. cloiophylla tends to shade out Arthrocardia sp. when it becomes dense. In the lower balanoid the canopy species Gigartina radula is completely dominant probably because of both its large size and the extremely rapid growth it exhibits (see p.165). Although free space does exist between the holdfasts of G. radula the prostrate fronds completely cover the substrate at low tide and during submersion a whiplash effect of the fronds is likely (c.f. Dayton, 1975). The understorey species C. clavulatum and G. stiriata are both restricted primarily to the lower balanoid and reach peak biomass out of phase with G. radula. This too may be attributable to a light excluding effect by the larger species although different growth patterns may also be involved.

G. pristoides and Ulva sp. are both abundant in the mid balanoid zone. Their density suggests possibly considerable competition for both space and light. Ulva sp. however is a rapidly growing, opportunist species (Bokenham and Stephenson, 1938) and tends to appear wherever free space becomes available. For example areas in the cochlear zone at Seapoint and the subtidal Plocamium fringe at Froggy Pond B were cleared during field-work for part I of this thesis and were subsequently colonized by Ulva sp. G. pristoides seems to dominate the middle balanoid while Ulva sp. exploits seasonal and long-term declines in Gelidium biomass. Biomass of Ulva peaks only after G. pristoides begins to decline (see fig.2.1). Likewise biomass of G. pristoides was high in 1976 and low in 1977, allowing Ulva sp. to attain higher biomass in 1977.

Porphyra capensis is the only macrophyte species present in the upper balanoid zone and never occupied more than 30-40 % of the space available. Competition obviously has no influence on the biomass of this species.

Competition for light and space thus appear to be greatest in the lower zones of the beach, where species richness is greater, and to have a larger effect on sub-dominant species. Correlation of biomass with abiotic factors was significantly lower for the sub-dominant species ($P < 0,05$). It seems however that fluctuations of subdominant biomass may be explained in terms of overwhelming competition by the dominant species in the various zones.

Thus biomass of four of the five dominant species was high in 1976 while the opportunist Ulva sp. and all four subdominants exhibited higher biomass in 1977.

Dominance in each zone is clearly attributable to one or two species. Furthermore, competition between dominant species in the same zone is reduced by differences in life history which result in peak biomass occurring in different months (eg. G. pristoides and Ulva sp.). Grazing in the cochlear and upper-middle balanoid zones prevents spores living long enough to escape mortality by their size. In the remaining zones however grazing effects are overridden by rapid growth and high biomass of algae and cannot explain fluctuations in the biomass of dominant algal species. In order to explain these fluctuations we must consider the influence of abiotic factors.

Abiotic factors

Dominant species all show good correlations with abiotic factors and tidal height appears to be the most important of these. Although biomass fluctuations may be explicable in terms of changes in the tidal regime, light intensity in particular also has an important influence (eg. the high correlation of biomass of Ulva sp. and P. cloiophylla with seasonal light intensity). Yearly differences in overall biomass levels may be due, in part at least, to differences in tidal conditions as described. Although periods of particularly high biomass of dominant species appear to be related to the tidal patterns the regularity of this correlation may only be confirmed by a longer term monitoring programme. Other irregular factors such as offshore current conditions, which can affect settlement, are probably also important.

In order to understand the influence of these three abiotic factors on biomass and possible reasons for the overriding influence of tidal height in particular, we must examine their direct effects in more detail. Productivity of algae is, of course related to factors affecting photosynthesis. As suggested above (p. 133) the influence of air temperature is minimised as low tides occur in the early morning and the most important factors are light intensity, sea temperature and the degree of desiccation. Thus seasonal fluctuations in algal biomass have been correlated with light and temperature (Conover, 1964; Earle, 1969; Croley and Dawes, 1970; Mathieson et al, 1976) and with seasonal tidal effects (Lawson, 1957; Umamaheswararao and Sreeramulu, 1964; Mshigeni, 1977).

1. Tidal conditions.

Table 2.1 reveals that the height of low tides was the most important abiotic factor affecting biomass for six out of nine species, including three of the dominants (c.f. Lawson, 1957). This is in indirect agreement with the findings of Schonbeck and Norton (1978). The Fucoid algae they examined were limited at the top of the shore by the degree of exposure to air which, when coinciding with drying conditions, lead to damage of the tissues. In the Cape tides are semi-diurnal and spring low tides occur between 0800 hrs. and 09.30 hrs. throughout the year so that the frequency of mid-day extreme low tides does not change seasonally (c.f. Mshigeni, 1977). However, the range of height for low tides varies from year to year and there was a pronounced seasonal pattern of higher low tides in summer than in winter during each year of the study period (fig. 2.3). These variations in the height of low tides corresponded particularly well to seasonal and yearly fluctuations of dominant species biomass (p. 149). During 1979 however tides were much higher during the winter months. Although sampling had been discontinued it was obvious that winter biomass of G. radula was higher than in the winters of previous years while there was no late summer "bloom" of G. radula. Although sunlight and air temperature follow a regular cycle, tidal changes are less consistent. It is apparently the interplay between these cycles which influences algal standing crop. The occurrence of higher low tides in summer produces ideal physical conditions leading to very high productivity, as during 1976. When such tidal

conditions prevail in winter however, biomass values are intermediate, being high for winter conditions but well below those described above.

The seasonal occurrence of higher low tides has two important effects which may influence productivity: zones are submerged for longer periods during each tidal cycle and zones above MHWN which are not submerged during every high tide are wetted more frequently each month. These effects are particularly marked in the lower zones. If the three dominant species which correlate best with tidal height are considered, correlation with biomass is found to decrease for the species higher upshore. Thus correlation is best for G. radula (lower balanoid), declines for G. pristoides (mid-balanoid) and is lowest for the upper balanoid species P. capensis (Table 2.1).

Both prolonged submergence and more frequent wetting of higher zones may cause an upward extension of vertical range (see below) and may influence photosynthetic rates and thus biomass within zones already occupied. G. radula and several other intertidal algae at Dalebrook have been found to exhibit higher photosynthetic rates during submersion at 1 m depth than at the surface (Fielding, unpublished data). This is presumably related to light intensities at various depths. The occurrence of higher low tides may thus have a direct effect on photosynthesis by increasing the depth of submersion.

Prolonged submergence may also influence photosynthesis by ameliorating the high desiccation rates of summer which are particularly great locally due to frequent S.E. winds. Brown and Johnson (1964) and Brinkhuis (1977b) found photosynthetic rates of intertidal algae to be very similar when in air and when submerged. It has however been found that at least some mid and upper shore species attain maximum photosynthesis after a period of desiccation (Mathieson and Burns, 1971). This may be extremely important as low natural rates of desiccation may result in some species fixing the bulk of their carbon requirements in air (Johnson et al, 1974). A relationship has, however, been demonstrated between the ability to resume photosynthesis after desiccation and vertical zonation (Schonbeck and Norton, 1978). Low shore intertidal species suffer reduced photosynthesis

when desiccated and photosynthesis of even upper shore species declines rapidly beyond the optimum degree of desiccation (Johnson et al, 1974). Longer periods of submergence may therefore reduce desiccation of low shore species such as Gigartina radula and cause the degree of desiccation of upper shore species such as Porphyra capensis to remain below critical levels for more prolonged periods. Both of these effects would result in higher photosynthetic rates during periods of higher low tides and thus close correlations between biomass and tidal height (Table 2.1).

Extended periods of submersion may also have a negative effect on biomass if they exceed the tolerance of a species. If intertidal algae do not experience a regular period of drying of suitable duration weight loss and death may occur (Biebl, 1962; Ogata and Schramm, 1971). Negative correlation of the biomass of C. erinaceum and C. clavulatum with tidal height (Table 2.1) may thus be due to excessive submergence, leading to reduced gas exchange and anoxia (Mntangi and Farrar, 1978). This effect may also account for an upshore shift in zonation of G. stiriata during summer (see fig. 2.6A and below).

2. Light

Light intensity may be expected to directly influence photosynthetic rates and thus productivity. However biomass of only two species was correlated best with light intensity (Table 2.1). Algae are particularly sensitive to light (Levyns, 1924) as indicated by the negative correlation between biomass of Ulva sp. and seasonal light intensities (Table 2.1). This is particularly interesting as it supports the findings of Branch (unpublished data) that artificial shading allows the opportunistic Ulva sp. to grow in zones where it does not normally occur.

The absence of negative correlations with light for other species however suggests that intensities are above critical levels only for Ulva sp. Low correlations with light for other species (Table 2.1) point to a surprisingly weak influence on productivity. This is explicable by a temperature based seasonal adaptation to low winter light intensities so that saturation and optimum light intensities decrease during autumn and winter (Mathieson and Burns, 1971; Brinkhuis, 1977a, b). This results in higher rates of photosynthesis in

winter than would be possible without such compensation. Hence correlations between seasonal light and biomass fluctuations are reduced and masked by the response of photosynthesis to other factors (c.f. Table 2.1). Biomass/light correlations may also be reduced by dark fixation of carbon as has been reported for phytoplankton (Morris et al, 1971; Taguchi and Platt, 1976).

Nevertheless photosynthesis does tend to be more rapid when the photosynthetic potential is higher in spring and summer (Himmelman and Carefoot, 1975; King and Schramm, 1976; Brinkhuis, 1977a). This pattern corresponds to seasonal growth patterns and for Pterosiphonia cloiophylla overrides the influence of other abiotic factors (Table 2.1).

3. Temperature

G. stiriata was the only species for which variations in biomass correlated best with seasonal sea temperatures (Table 2.1). Although a synergistic temperature effect causing winter photosynthetic rates at low temperatures to attain similar levels to summer rates at higher temperatures has been suggested (Brinkhuis, 1977a), it seems that light effects are more important (Brinkhuis, 1977b). Seasonal increases in sea temperature in the Cape are synchronous with light intensity increases (fig. 2.2) and may increase the ability of algae to utilize the greater amount of light available in summer rather than having a direct effect on photosynthetic rates.

To summarize, biomass of dominant species appears to be controlled to a large degree by abiotic factors, particularly tidal conditions. Biomass of subdominant species varies in response to the competitive effect of the more abundant and generally larger dominant species. Consequently there is little correlation between subdominant biomass and abiotic factors. The correlations which were obtained indicate that seasonal increases in the height of low tides correlate with an increase in dominant species biomass and a decrease in subdominant species biomass.

Zonation changes

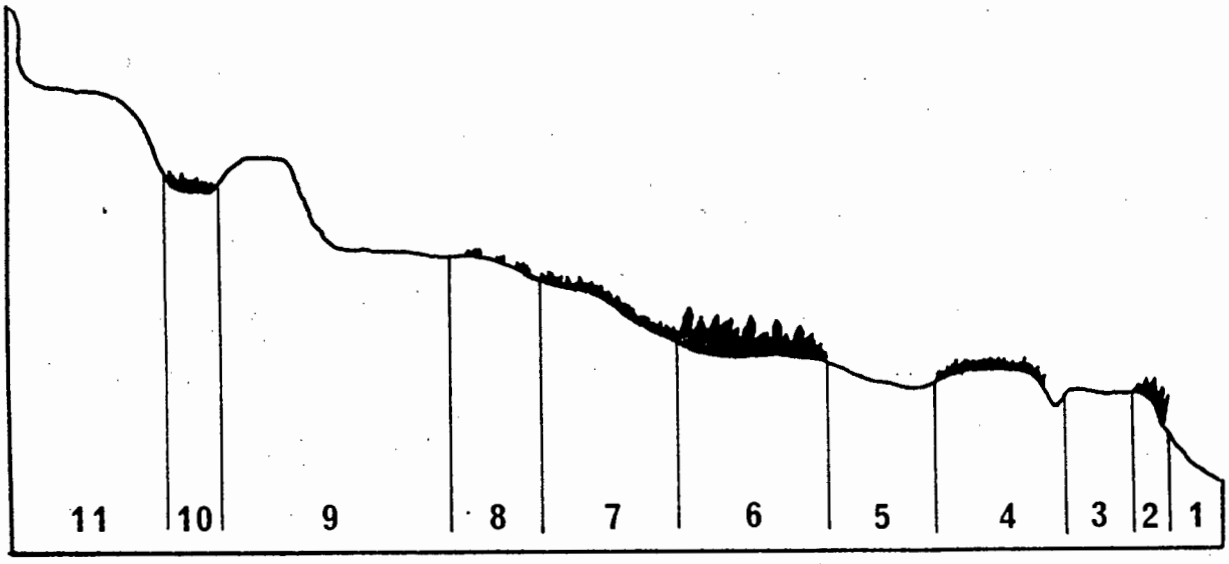
Almost all increases in biomass were accompanied by modifications to distribution (figs. 2.6A-G). In most cases this entailed an extension

of range into adjacent zones. The causes of intertidal algal zonation have been attributed to a number of factors. It is however currently accepted that lower zonation limits are determined by complex biological interactions, including competition, predation etc. while upper limits are determined by the ability of species to withstand increasing physiological stresses higher up the shore (see Connell, 1972 and Chapman, 1973 for reviews). In the present work extensions of vertical range were found to generally occur in an upshore direction in accordance with the findings of Lawson (1957) and Mshigeni (1977). This may be due to an amelioration of increasing summer desiccation effects by a higher tidal regime. Downshore extensions were exhibited only by two species. Gigartina radula in summer extended both up and down the shore, despite presumed predation by Oxystele spp. (fig. 2.6F). It may be assumed that this large fronded species can successfully outcompete the smaller downshore species for light and, with the vigorous growth exhibited, probably for space as well. A winter reduction in the number and size of fronds allows these smaller species, along with the opportunist Ulva sp., to regain dominance during the rest of the year. The second species to exhibit a downshore extension was Centroceras clavulatum (fig. 2.6G). Reduced summer biomass of this species may be attributed to the smothering effect of G. radula which occupies the same zones. During winter the extensive reduction of biomass for all other species allows a temporary downshore extension of C. clavulatum when its biomass is relatively high (fig. 2.1). Extensions of this and the other two subdominant species C. erinaceum and G. stiriata, which are also present at generally low biomass probably indicate an opportunistic exploitation of space left by seasonal recession of the dominant species. Thus seasonal changes in vertical range may also be explained in terms of the response of dominant species to abiotic factors and of subdominant species to varying competitive pressure from the dominant species.

A summer upshore shift in the range of G. stiriata in response to raised tidal levels agrees with the findings of Mshigeni (1977) for Hypnea musciformis in Hawaii and Knight and Parke (1931, cited by Lawson, 1957) for algae in the Isle of Man. This is augmented by increased competition by G. radula in the lower balanoid. As biomass of G. radula becomes high G. stiriata disappears from the lower balanoid (figs. 2.6A, F).

For five species extensions of range were accompanied or preceded by a downshore shift of the region of maximum density a month or so before the range extended upwards (p.158). This is likely to

Schematic representation of algal community structure at Dalebrook.



1. Subtidal, grazing high, algal diversity high but biomass low.
2. Lower cochlear fringe, algal diversity low, biomass of Arthrocardia and Pterosiphonia moderately high.
3. Lower cochlear, limpet density very high,grazing intense. Algal biomass and diversity extremely low.
4. Middle cochlear, limpet density low. High algal biomass. Gelidium and Ulva dominate and compete.
5. Upper cochlear, limpet density intermediate. Algal biomass low except in summer when rapid growth and settlement of Gigartina radula outstrip grazing.
6. Lower balanoid, physical conditions optimal. Grazing intermediate (Oxystele), growth rates high, biomass of algae very high, dominated by G. radula. Zonation and biomass regulated by response of dominants to seasonal changes in abiotic factors and of subdominants to competition.
7. Middle-balanoid, algal biomass high, dominated by Gelidium and Ulva. Abiotic conditions and competition important.
8. Upper-middle balanoid, conditions harsh, growth rates low. Grazing by Oxystele leads to low algal biomass.

9.and 11. Upper balanoid and lower Littorina zones, conditions very harsh. Generally only Porphyra is present and may attain high biomass.

10. Temporary exploitation of unoccupied space by the tough, rapidly growing opportunist Ulva which is outcompeted by Gelidium lower down.

be related to an increase in photosynthesis with depth, described above. As low tides become higher the depth and duration of submersion increase most rapidly in the lower zones, optimising conditions for photosynthesis. In succeeding months low tides continue to become higher and this optimisation of conditions extends upshore beyond the normal limits of range.

The structure and dynamics of the algal community at Dalebrook are controlled by both abiotic and biotic factors leading to seasonal and long term fluctuations in species biomass. Abiotic/biotic factors assume different degrees of importance in the different zones. These effects are summarized schematically on page 174.

Calorific value

Considerable fluctuations in the calorific value of the algae examined occurred during the year. Although a pattern was not clear for some species, values were generally maximal in summer/autumn and minimal in spring/winter. Contradictory evidence exists in the literature concerning the seasonality of algal calorific values. Golley (1961) has reviewed the literature on the calorific content of ecological materials and found that there were significant differences in values obtained for terrestrial plants collected in different seasons. Paine and Vadas (1969), however, found that seasonality made no difference to calorific content in a wide range of algae although they did find phylogenetic trends. Mann (1972) found seasonal variations of up to 50 % in the percentage dry weight of kelps. Calorific values of dry material varied by about 10 % and on the basis of these findings marked seasonal in the calorific value of fresh material were predicted. Subsequently Himmelman and Carefoot (1975) found distinct annual cycles in both dry weight and calorific value of three intertidal species in Vancouver and seasonal changes in the calorific value of Fucaceae were found by Breton-Provencher and Cardinal (1976).

Seasonal changes in the chemical composition of algae are well documented and alterations in the ratio of proteins to more energy rich carbohydrates and fats may be expected to affect calorific values. Algae generally utilize various carbohydrates as storage compounds. The characteristic storage products of Rhodophytes (8 of the 9 species

monitored) are floridian starch, and amylopectin (Dixon, 1973) while Ulva spp. use both amylopectins and amylose (Craigie, 1974). Most work on chemical changes in sub and intertidal algae has been carried out on the brown algae which are so prominent in the Northern hemisphere. The Phaeophyta generally use mannitol and the polysaccharide laminarin as storage compounds but seasonal changes in the abundance of these compounds implies similar changes in the storage products of red and green algae.

During periods of rapid growth storage carbohydrates tend to be rapidly utilised resulting in minimum values during spring and early summer, maximum values occurring in late summer or autumn as growth rates decrease (Black, 1948, 1949, 1950; MacPherson and Young, 1952; Medcalf et al, 1975). Laminaria longicruris exhibits maximum growth rates during winter but it too experiences maximum carbohydrate content as growth rates decrease (Chapman and Craigie, 1977, 1978).

The role of lipids as reserve substances in algae is doubtful and their importance probably lies in the formation of biological membranes (Wood, 1974). There are however some data on seasonal fluctuations in lipids. Although Collyer and Fogg (1955) found up to 40 % of dry mass of Prophyridium cruentum was formed by fats, lipid content is generally low (1-6 %, Dawes et al, 1974, Munda, 1962) and appears to vary in a similar manner to carbohydrates. Minimum values occur at the beginning of the growth period and maximum values towards the end of growth in late summer (Wort, 1955; Munda, 1962; Idler and Wiseman, 1970; Zavodnik, 1973a, b).

Conversely protein values tend to be maximal during rapid growth and decline towards the end of summer (Black, 1948, 1949, 1950; Munda, 1962, Zavodnik, 1973a, b). Consequently the protein/carbohydrate ratio changes seasonally reaching a maximum in the spring/early summer periods of rapid growth and declining with growth rates during summer to minimum values in autumn (Dawes et al, 1974; Dawes, 1977).

Apart from the effect of growth period the reproductive cycle also influences calorific values, though the implications of this are not perfectly understood as yet. Dawes et al (1974) and Dawes (1977)

found that carbohydrate values decreased during the early reproductive period. Although this is unexplained it seems likely that this may be due to the utilisation of carbohydrates in the formation of reproductive structures. Himmelman and Carefoot (1975) found higher calorific values during sporulation. This was thought to be due in part to the presence of energy rich spores.

Calorific values may be expected to be higher when the protein/carbohydrate ratio is lowest. During this study it was found that values did generally reach a maximum between mid summer and autumn. Although no analyses of chemical composition were undertaken this corresponds to periods of predicted low values of the protein:carbohydrate/lipid ratio. The suggestion of an inverse relationship between growth rate and calorific value is supported by correlation between biomass and calorific content. Although correlation was best at lag 0 for two species the remaining species showed best correlation at lag 2 or 3 (5 species) or a negative correlation at lag 2 (2 species). This indicates accumulation of carbohydrates and fats in the post rapid growth period (correlation at lag 2/3) and utilization of these storage products as growth increases (negative correlation at lag 2).

Calorific value of algae is, of course, of prime importance to macrophyte herbivores. Dayton (1975) observed that densities of herbivores were generally well below the apparent carrying capacity of algal standing crop. The possibility of sometimes extreme changes in the energetic quality of algae however indicates that carrying capacity may vary in more subtle ways than a simple change of standing crop. Furthermore it has been found that some herbivores select algae of intermediate energetic value as food (Paine and Vadas, 1969). Again, although this is not felt to be important in the present situation it is possible that seasonal changes in calorific content of algae may influence herbivore/algal relationships.

SUMMARY

1. Approximately 85 % of intertidal biomass at Dalebrook was found to be formed by 9 species including 5 dominant species: (Gelidium pristoides, Gigartina radula, Porphyra capensis, Pterosiphonia cloiophylla and Ulva sp.) and 4 sub-dominant species (Arthrocardia sp., Centroceras clavulatum, Chaetangium erinaceum and Gigartina stiriata).

2. No seasonal changes in species dominance were observed and no major algal zones were found to disappear seasonally. However, a transient Porphyra capensis zone appeared high on the shore in October 1976 and disappeared only after two years.

3. Large biomass changes were found to occur on both a seasonal and long-term basis for all species. Maximum biomass generally occurred in summer and was accompanied by extensions of vertical range. Biomass of all dominants except Ulva sp. was highest in 1976. Grazing effects are thought to be important mainly in specific regions of the beach and competition between dominants is reduced by peak biomass occurring out of phase where two dominant species share a zone.

4. Variations in biomass and vertical range of dominant species show good correlations with abiotic factors, especially the height of low tides. All dominant species reach peak biomass during periods when low tides are high. This may be related to increased photosynthesis with depth during submersion.

   The biomass of subdominant species are out of phase with dominant species biomass and are probably controlled largely by competition effects. Zonational changes of subdominants may also be explained by competition.

5. Ash content of all species varies seasonally and is generally minimal in winter. Ash-free calorific values also vary on a seasonal basis, reaching a maximum in late summer/autumn. This coincides with periods of predicted low values of the protein:

carbohydrate/fat ratio caused by rapid growth. Thus calorific value was found to become maximal in the post rapid growth period, as biomass declined, or to exhibit an inverse relationship with biomass.

CHAPTER 6 : POPULATION DYNAMICS AND SIZE DEPENDENT ZONATION OF LITTORINA AFRICANA KNYSNAENSIS PHIL. (GASTROPODA : PROSOBRANCHIA).

INTRODUCTION

The periwinkle Littorina africana knysnaensis occurs around the coast of South Africa from Zululand to Luderitz (Day, 1979). The high resistance to desiccation of L. a. knysnaensis is well known (Broekhuysen, 1941; Brown, 1960) and it is abundant even above EHWS on exposed rocky shores, dominating the beach above HWN and characterising the Littorina zone. L. a. knysnaensis is important in energy flow in the intertidal community because of this zonational dominance. At present there are no data available on the population dynamics of this species and these are essential for an understanding of community energetics on the upper shore. Consequently seasonal and long-term changes in the population size and age structure were examined at Dalebrook, along with growth rates, to elucidate the nature of population changes.

Populations of L. a. knysnaensis show a vertical size gradient on the shore as has been found for other species of littorinids (eg. Chow, 1975; Heller, 1976; Raffaelli and Hughes, 1978). The subject of size gradients has been reviewed by Vermeij (1972) but the gradient exhibited by L. a. knysnaensis is the reverse of his model for upper shore species as mean size decreases in an upshore direction. Size gradients are an important feature of the population, having a direct influence on biomass distribution, and the mechanisms maintaining this size gradient were investigated.

METHODS

1. Sampling

Preliminary observations revealed that the distribution of L. a. knysnaensis is so clumped that no accurate estimates of population size can be made from data on sub-sampling of small areas. An isolated population was therefore selected, occupying an area of approximately 160 m^2, and separated from adjacent populations by bare rocks and gulleys.

The population considered showed a size gradient of decreasing shell length up the shore. The lower, mid and upper Littorina zones were dominated by different size classes of animals. These zones were termed A, B and C respectively and, although they were not physically isolated from one another, the snails occurring in each zone are referred to as separate "sub-populations" for convenience. Zone A was dominated by large animals and zone B by medium sized animals. Zone C is the highest of the three and is formed by a set of large boulders inhabited almost exclusively by small animals.

Sampling was carried out during spring low tides every six weeks for 15 months from November 1976 to January 1978. During each sampling session the entire population of each zone was counted. This required two days but careful checks indicated that overnight migration between zones was negligible. Size frequency histograms were derived every six weeks for each zone by measuring the shell lengths of approximately 300 animals from each zone using vernier callipers. Acidised dry weights were obtained by removing the shell using 1M HCl and drying for 48 hr. at 60°C. Regressions of length against acidised dry body weight were derived for autumn (Mar. 1977), winter (June, 1977), spring (Sept. 1977) and summer (Jan. 1978). The data for these regressions were subjected to log/log conversion and t-tests used to compare their slopes and intercepts.

2. Maintenance of size gradients

The size gradient exhibited was investigated by examining the hypothesis that juvenile settlement occurs primarily in zone C and is followed by gradual downshore migration of the growing animals. If

this is so then zones A and C may offer sub-optimal conditions for juveniles and adults respectively. Two further hypotheses were therefore tested; that zone A is unsuitable for juveniles due to a higher intensity of wave action, and that adults, or growing animals migrate down from zone C in response to increased food availability farther downshore.

(a) Migration

It is extremely difficult to mark individual snails for periods long enough to reveal age dependent migration (eg. see Darby, 1964), but individuals may be marked with paint spots for up to several months. This allows the observation of dispersal of specific size classes of animals placed in zones where they do not normally occur. Samples of 100 juveniles (< 5mm) and 100 adults (> 7mm) were collected from zones C and A respectively, marked and released in the reverse zones. The release spot served as a reference point from which the distance and compass bearing of each recovered snail were taken daily for 9 days. Control experiments were carried out by marking further samples of adults and juveniles and releasing them in the zones in which they were originally collected.

(b) Tethering experiments

If zones not normally occupied by a particular size class are indeed sub-optimal for that class then a reduced "ecological performance" may be expected if animals are forced to remain in such zones. This may be revealed as weight loss or decreased growth rates or as more subtle effects such as reduced fecundity or delayed sexual maturation.

To investigate this 100 juveniles and 100 adults were collected from the appropriate zones. Light nylon leads of 20 cm were attached to the shell of each animal using an epoxy glue. 50 animals of each size class were then tethered in zones A and C by fixing the free end of the lead to the substrate with fibre-glass resin. The animals tethered in the zones where they were collected thus served as controls for comparison with the transferred animals. The tethered animals were recovered after one month and length/acidised dry weight regressions derived for each sample. t-tests were used to compare the slopes and intercepts of the curves of the adult samples and of the two juvenile samples.

(c) Tenacity and wave action

The relationship between snail size and tenacity was examined using a technique adapted from Hylleberg and Christensen (1978). Very light cotton leads were glued to the shells of animals covering a range of sizes. The snails were then allowed to adhere to glass plates in running sea water. Tenacity was measured by running the thread vertically upwards over a well oiled wheel and hooking the free end to a small dish which was slowly filled with sand until the snail was pulled free of the glass plate. The dish plus sand were then weighed and the combined weight plotted against snail length.

Wave action in the three zones was measured on an incoming tide using a turbulometer (Field, 1968). Readings were obtained for a minimum of 20 waves over a 5 minute period in each zone. The means for the 10 highest readings obtained in each zone were used as a comparative index of exposure following Field (1968).

(d) Food availability

The hardness of the substrate at Dalebrook renders measurement of microphytic food availability from rock scrapings impossible. An alternative estimate was therefore obtained by measuring the rate of settlement of primary producers on a clean substrate. Polyethylene strips of 15 x 3 cm were roughened with fine sandpaper and then fixed in each of the Littorina sub-zones using fibre-glass matting and resin. The strips were recollected after 90 days and cut into 3 x 5 cm sections. Chlorophyll on these sections was extracted by submersing them in 90 % acetone for 24 hours in a refrigerator after sonification to break down the cell walls. During this period the tubes containing the samples were wrapped in silver foil to prevent light induced breakdown of the chlorophyll. Chlorophyll a concentration was derived by measuring the optic density of the centrifuged chlorophyll extract at 663,645 and 630 nm using a spectrophotometer. These values were converted to mg chlorophyll a using the equation

$$C = 11{,}64E_{663} - 2{,}16E_{645} + 0{,}10E_{630}$$ (Strickland and Parsons, 1968)

where E is the extinction value at the wavelength given by the subscript.

3. Growth rates

To derive accurate growth rates mark and recapture experiments were carried out. The small size of the animals and the large population size render marking of individuals impossible. Experiments were therefore carried out by marking samples of animals of particular size classes with paint spots. Normal distribution (checked for in each sample) allowed the derivation of a mean length for each marked sample. The growth rates derived are thus changes in the mean value for samples.

Two separate aspects of growth were investigated:

(a) Annual growth

Three size classes were selected to represent small, medium and large animals: 2-3 mm, 5-6 mm and 8-9 mm respectively. A total of approximately 200 animals were marked with a distinct colour for each size class and the mean length (measured to 0,05 mm) derived. No mortality due to marking was observed. The samples were replaced on the beach and at three periods during the following seven months the marked animals were recovered and the mean length for each size class derived. Remarking of animals was carried out whenever necessary. The total size of the samples decreased with time due to mortality and removal of paint from some specimens. After seven months the number of remaining marked animals had become small and a duplicate experiment was run on new samples for a further seven months. This experiment began in July when few animals of 2-3 mm were present and animals of 3-4 mm were used to represent the small size class.

(b) Seasonal size specific growth rates

These were derived for the same three size classes as above. Additional samples of 100-150 animals for each size class were marked and growth over a period of 50-70 days during each season was derived and converted to mean length increment per day. Seasonal growth rates were thus derived for autumn (March 1978), winter (June 1978), spring (September 1978) and summer (December 1978).

RESULTS:

1. Size distribution and settlement

Fig. 2.9 summarizes the vertical size trend of L. a. knysnaensis on the shore. Data for Dalebrook are based on a typical month (Feb. 1977). Data for the remaining beaches are based on unpublished work by Miss. C. da Silva and indicate that there is a general trend on rocky beaches for the mean length of L. a. knysnaensis to decrease up the shore.

Histograms showing size distribution for 15-16 months in each of the zones examined are given in figs. 2.10 - 2.12.

Zones A - C are dominated by the 7-8, 6-7 and 4-5 mm size classes respectively, except during heavy settlement. The absence of animals 7 mm in zone B and, after June, of animals 5 mm in zone C is marked, reflecting a progressive downshore migration of animals as they grow larger (see below).

The presence of small animals (2-3 mm) throughout the sampling period indicates continuous recruitment. However distinct periods of heavy recruitment are obvious in all three zones.

(a) Small cohorts of mean length 2-3 mm appeared in October 1976 in zones A and B and soon merged with the main population (figs. 2.10 - 2.12). Although data are missing for this month for zone C it seems likely that a new cohort also appeared there.

Much larger scale settlement occurred in all zones in June 1977 and December 1977.

(b) The June Settlement comprised a cohort of 3-4 mm suggesting that recruitment began between the May and June sampling sessions.

This winter recruitment extended for several months and an ill-defined cohort still evident in September at zone B probably represents the end of this settlement period.

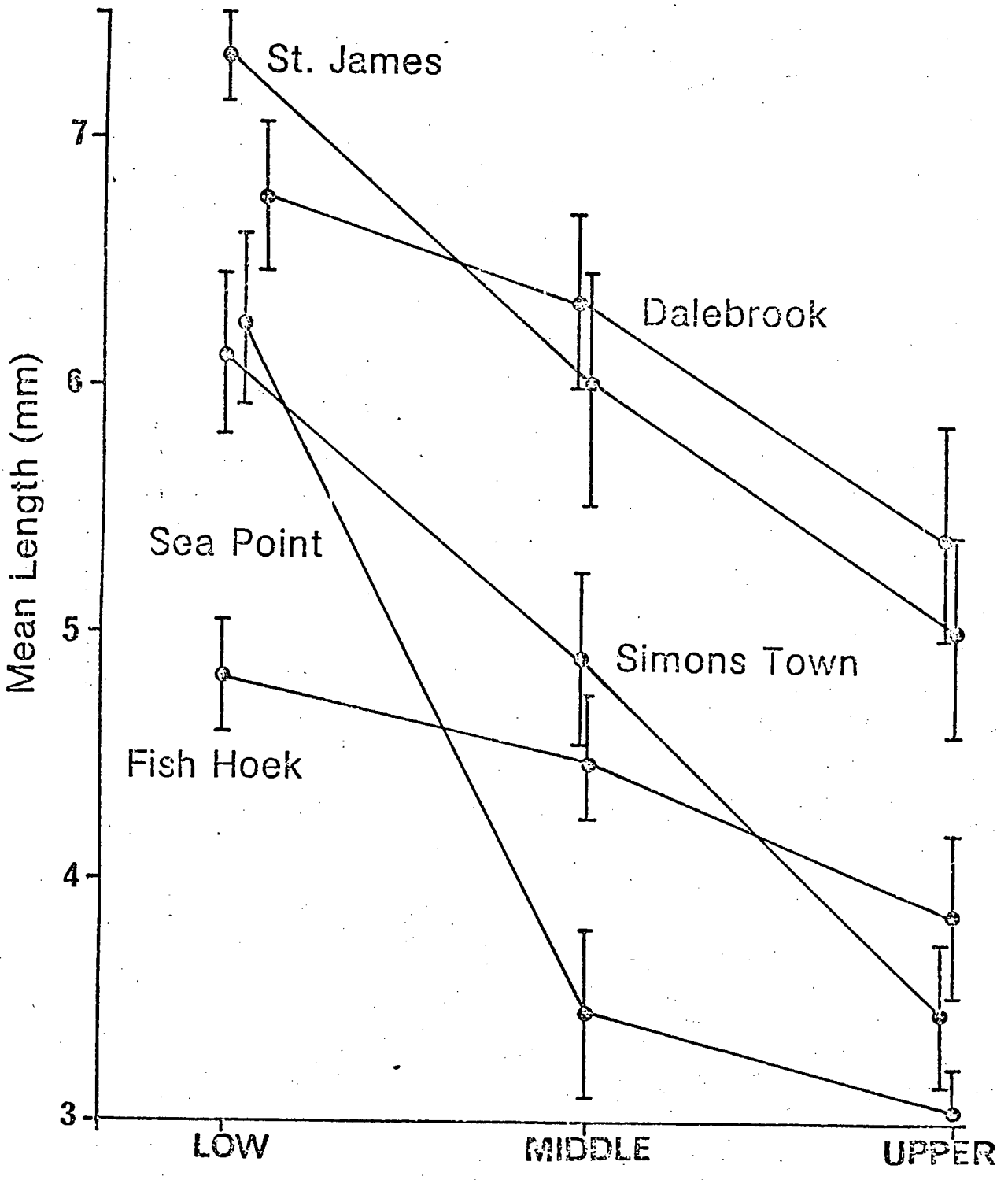


Fig. 2.9 : The relationship between mean length of Littorina africana knysnaensis populations and position on the shore. Information for beaches other than Dalebrook is based on unpublished data from Miss. C. Da Silva. Mean lengths are given ± S.D.

Fig. 2.10 : Size frequency distribution for Littorina africana knysnaensis in zone A at Dalebrook at six-weekly intervals from November 1976 to January 1978. N indicates sample size.

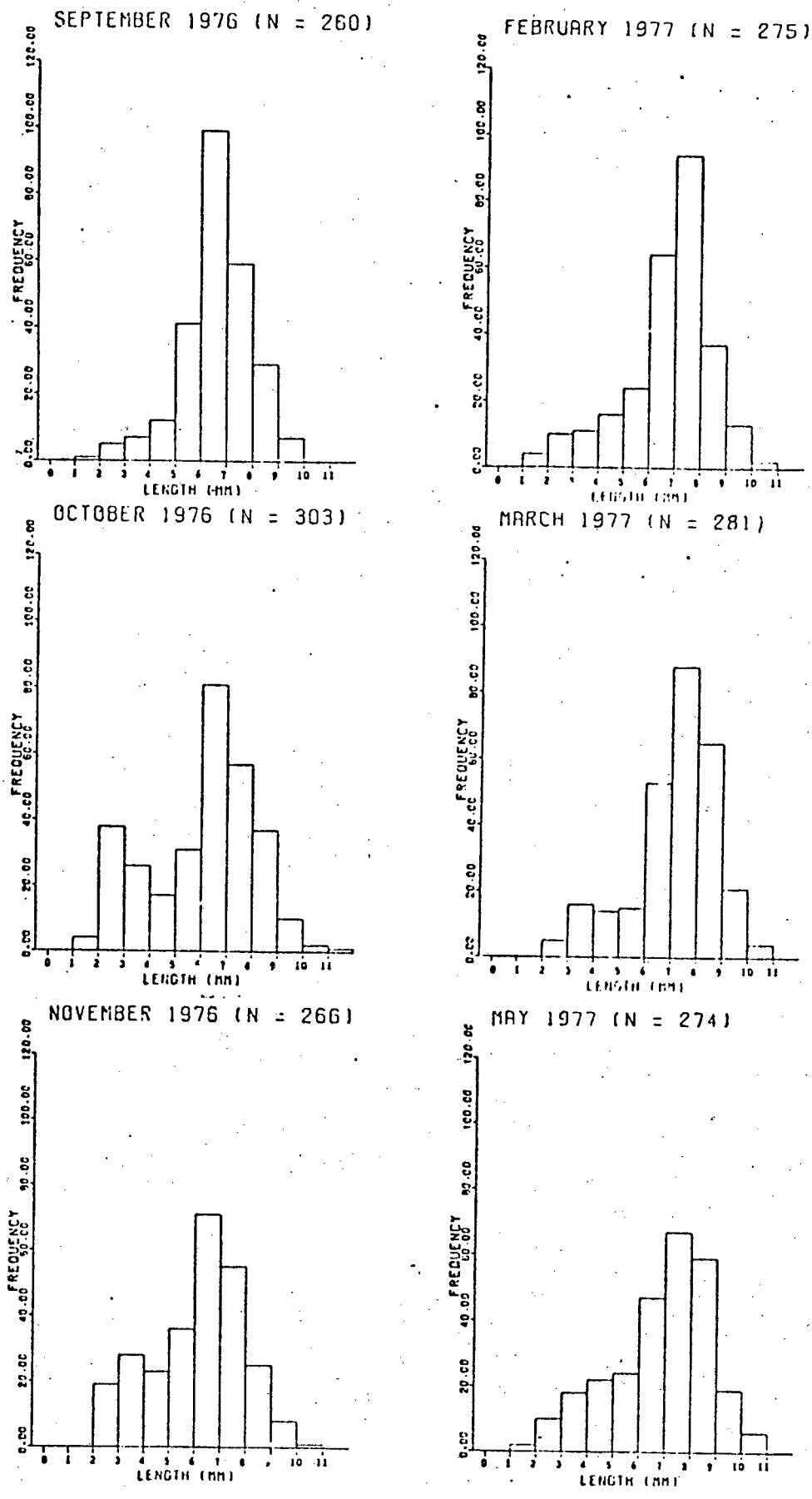

SEPTEMBER 1976 (N = 260)
FEBRUARY 1977 (N = 275)
OCTOBER 1976 (N = 303)
MARCH 1977 (N = 281)
NOVEMBER 1976 (N = 266)
MAY 1977 (N = 274)
FREQUENCY
LENGTH (MM)

Fig. 2.10. .

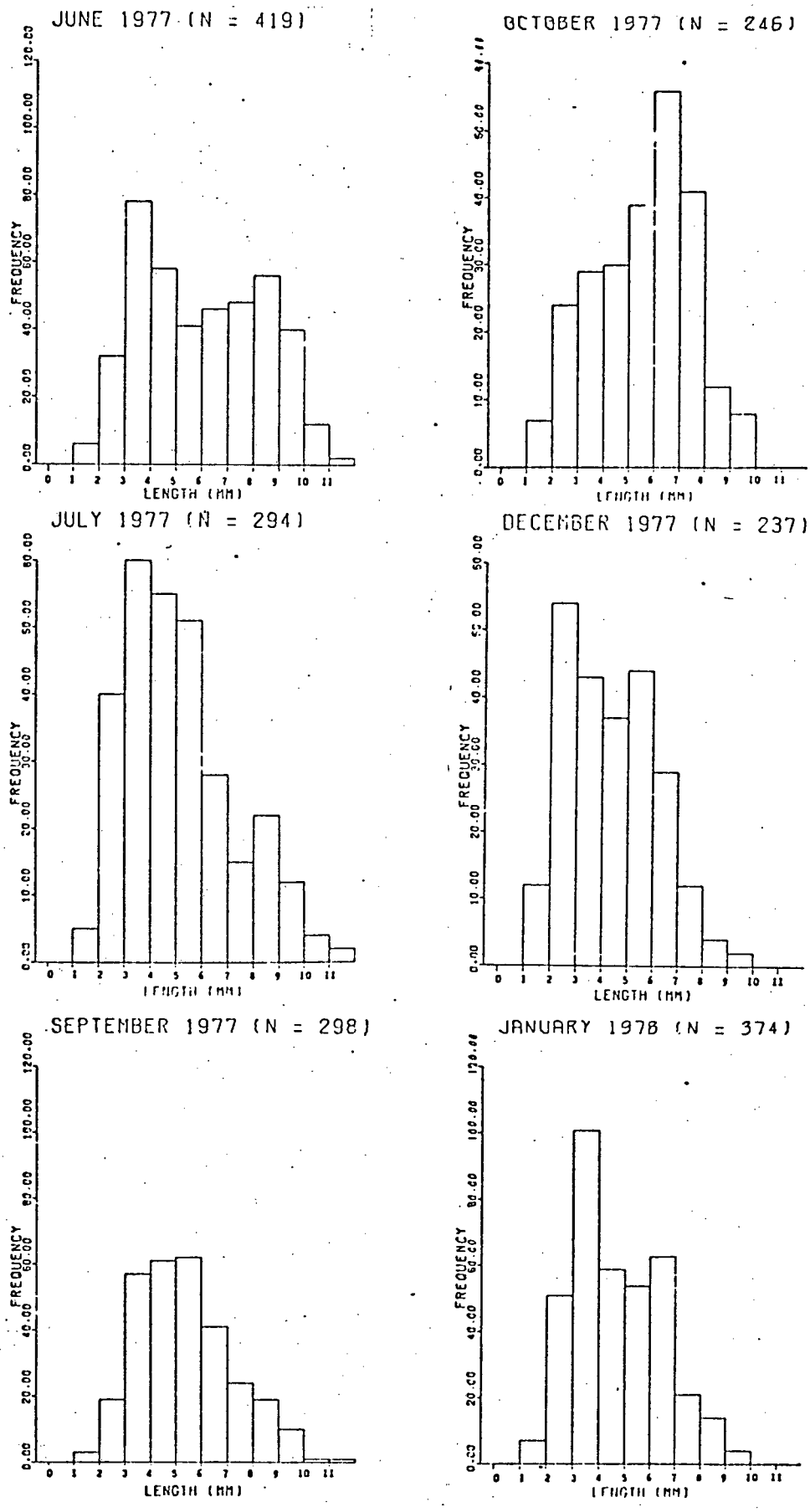


Fig. 2.10 (Cont'd)

Fig. 2.11 : Size frequency distribution for Littorina africana knysnaensis in zone B at Dalebrook at six-weekly intervals from September 1976 to January 1978. N indicates sample size.

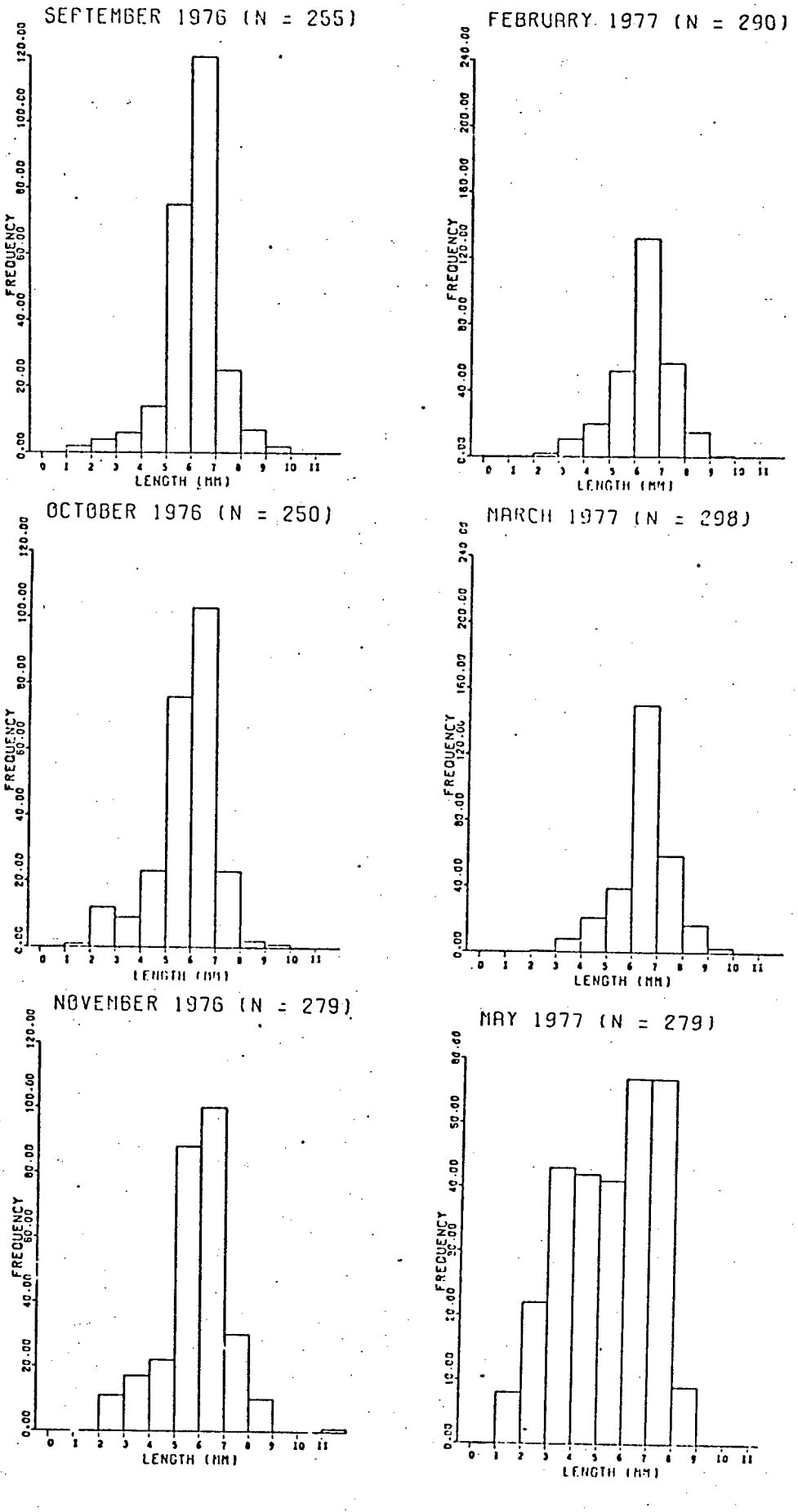

SEPTEMBER 1976 (N = 255)
FEBRUARY 1977 (N = 290)
OCTOBER 1976 (N = 250)
MARCH 1977 (N = 298)
NOVEMBER 1976 (N = 279)
MAY 1977 (N = 279)
FREQUENCY
LENGTH (MM)

Fig. 2.11

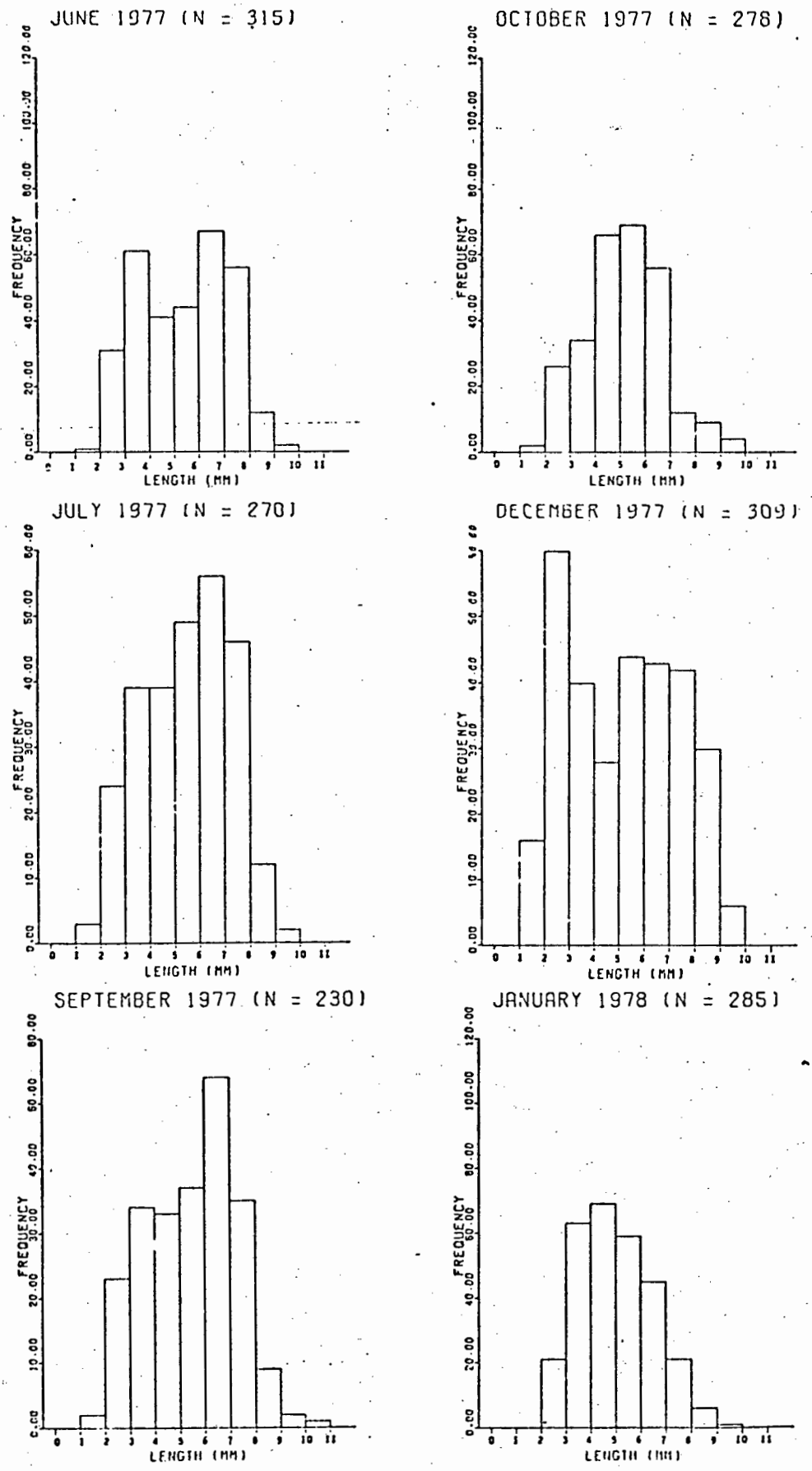


Fig. 2.11 (Cont'd)

Fig. 2.12 : Size frequency distribution for Littorina africana knysnaensis in zone C at Dalebrook at six-weekly intervals from November 1976 to January 1978. N indicates sample size.

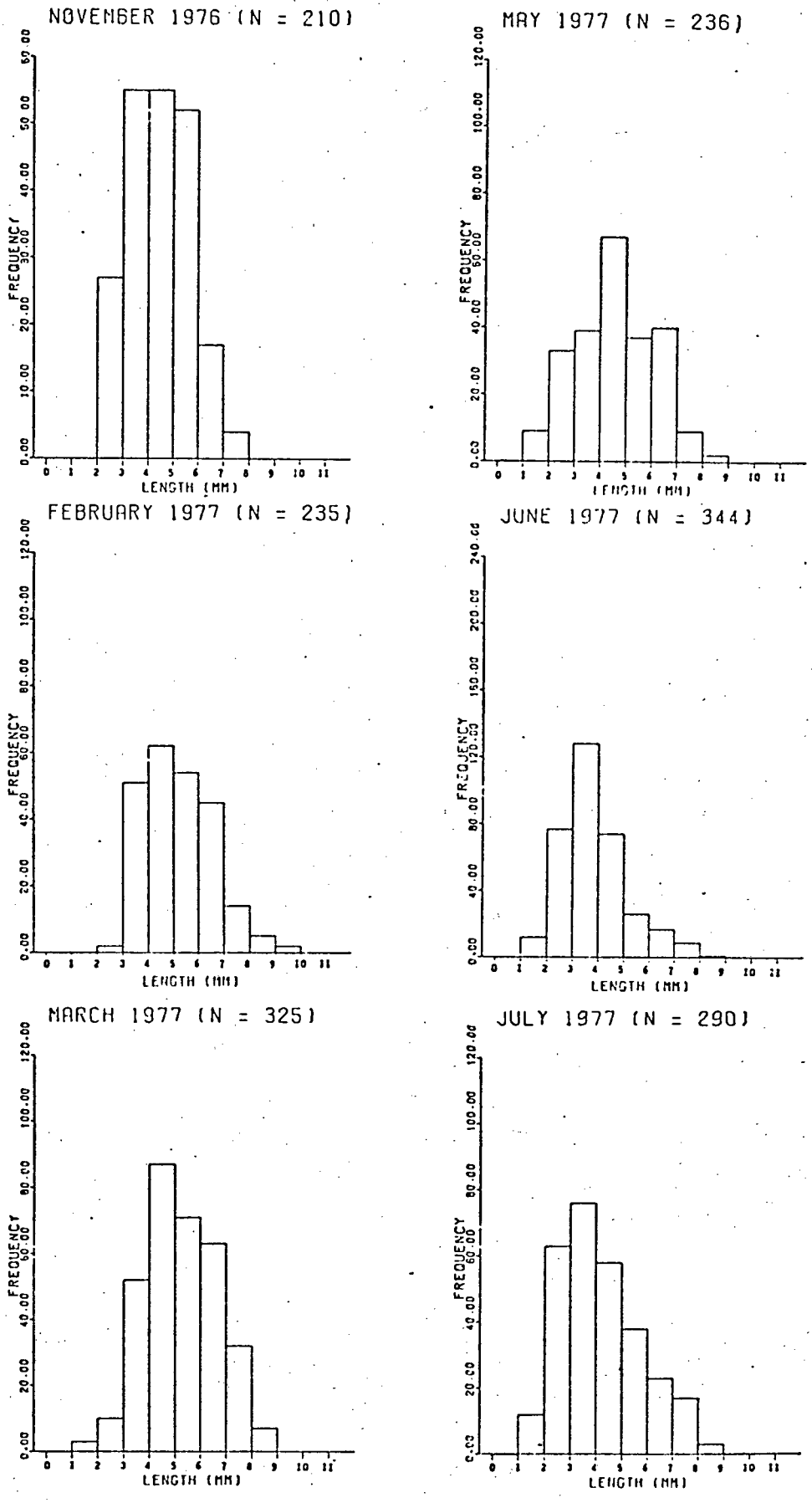

NOVEMBER 1976 (N = 210)
MAY 1977 (N = 236)
FEBRUARY 1977 (N = 235)
JUNE 1977 (N = 344)
MARCH 1977 (N = 325)
JULY 1977 (N = 290)
FREQUENCY
LENGTH (MM)

Fig. 2.12

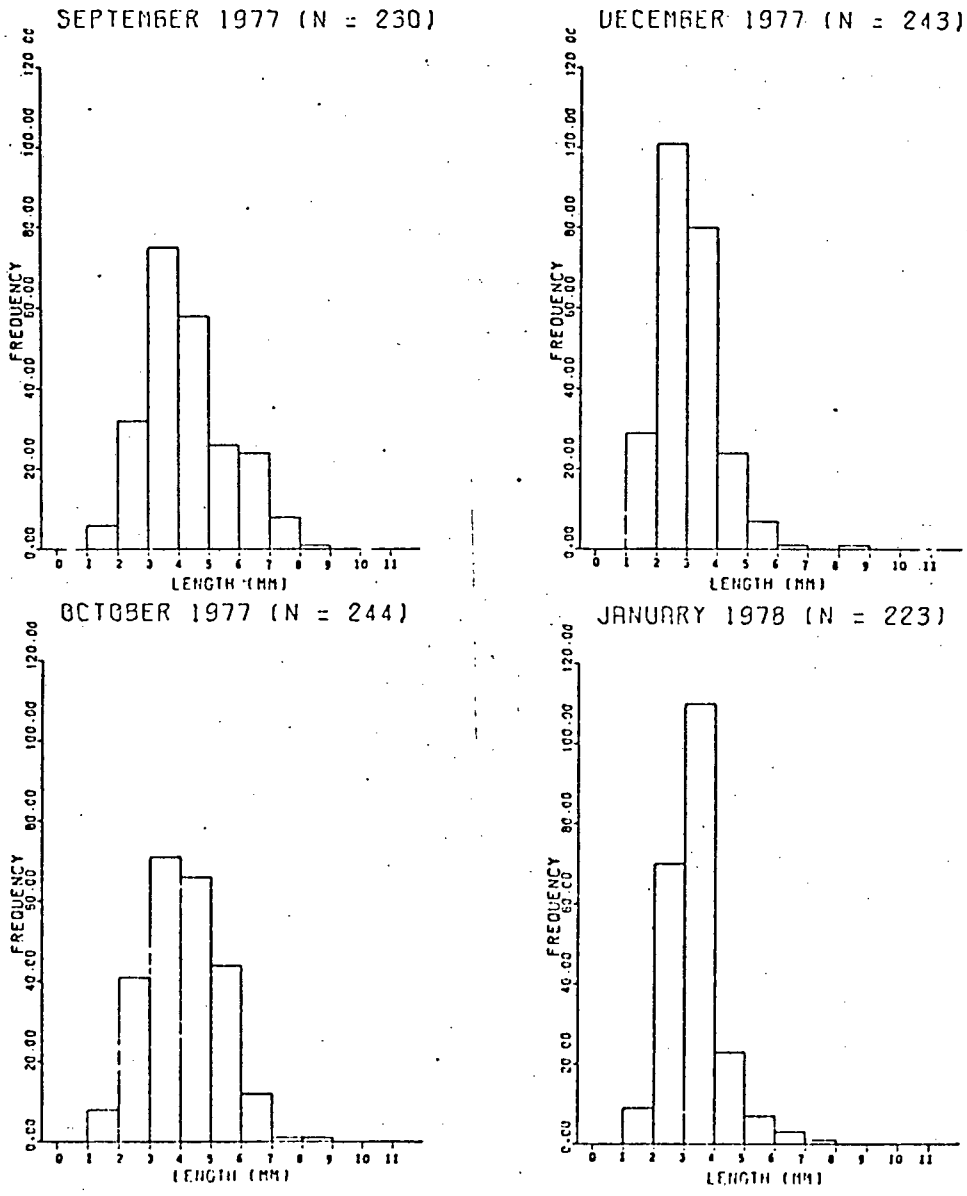


Fig. 2.12 (Cont'd)

(c) During December cohorts of 2-3 mm appeared in all zones. This settlement continued into January resulting in a further increase in numbers from December to January (fig. 2.22).

Rapid merging of cohorts and the effects of continuous recruitment render the use of polymodal analysis for growth rates inappropriate. The histograms do however indicate:

(i) the consistency of size distribution in each zone except during settlement and the permanent absence of more than a few large or medium animals from zones B and C respectively.

(ii) continuous recruitment revealed by the presence of juveniles throughout the year.

(iii) periods of higher recruitment during October 1976 and more markedly in June and December 1977. The months prior to and following the onset of winter settlement in May/June 1977 are therefore referred to as periods of light and heavy settlement respectively.

New cohorts appear at 2-3 or 3-4 mm. To assess settlement in each zone the number of juvenile animals of less than 4 mm was calculated from size frequencies data and the mean derived for light and heavy settlement periods. This is expressed as the percentage of total number of animals less than 4 mm in Table 2.2. Many larvae may die immediately after settlement. These data therefore indicate "successful" settlement in each zone, that is the number of animals which attain at least 1 mm in length after settling.

TABLE 2.2 : MEAN MONTHLY PERCENTAGE SETTLEMENT IN EACH ZONE AND OVERALL MORTALITY FOR LIGHT AND HEAVY SETTLEMENT PERIODS.

	TOTAL SETTLEMENT	ZONE SETTLEMENT AND % OF TOTAL A	B	C	OVERALL CHANGE IN POPULATION	% MONTHLY MORTALITY
Light settlement	1690	108,66 (6,43)	105,96 (6,27)	1475,30 (87,30)	-986	23,47
Heavy settlement	10509	747,19 (7,11)	3764,32 (35,82)	5997,49 (57,07)	+6206	17,87
Mean	6099	412,90 (6,77)	1283,23 (21,04)	4402,87 (72,19)	+2610	20,67

During light settlement recruitment occurred primarily in zone C (87,3 %). As settlement became heavier however the percentage of total

settlement in zone B increased considerably. On the assumption of no immigration or emigration from other populations a mean mortality may be estimated for these two periods. This was calculated as total population change minus recruitment (Table 2.2). The results of this are similar to monthly mortality rates recorded for Tegula funebralis by Paine (1969). Percent mortality was higher for the period of light settlement, and in combination with low settlement rates, lead to an overall decrease in numbers (see below).

2. Maintenance of size gradients

(a) Migration

Figs. 2.13 and 2.14 show the direction of dispersal of experimental and control animals 1, 5 and 9 days after release. Dispersal of juveniles placed in zone A (fig. 2.13) is clearly upshore. Local topography resulted in an initially less clear pattern for adults placed in zone C (fig. 2.14) but by day 5 a clear downshore trend was evident.

χ^2 tests indicate non-random dispersal of experimental animals ($P < 0,01$) but random dispersal of control animals, released within their normal zones ($P > 0,05$). Experimental animals also showed steady movement away from the release point. For control animals movement was random and mean distance from the release point quickly levelled off (figs. 2.15, 2.16). Dispersal was more rapid for adult animals due to their greater size and mobility.

(b) Tethering experiments

Figs. 2.17 - 2.20 give length/acidised dry weight regressions for adult and juvenile snails tethered in zones A and C. t-tests indicate no significant differences in slope between control and experimental samples for either juvenile or adult comparisons ($P > 0,05$). The y-intercept is however significantly higher for juveniles in zone C than in zone A and for adults in zone A than in zone C ($P < 0,01$) indicating reduced body weight for members of either size class when tethered in the inappropriate zone.

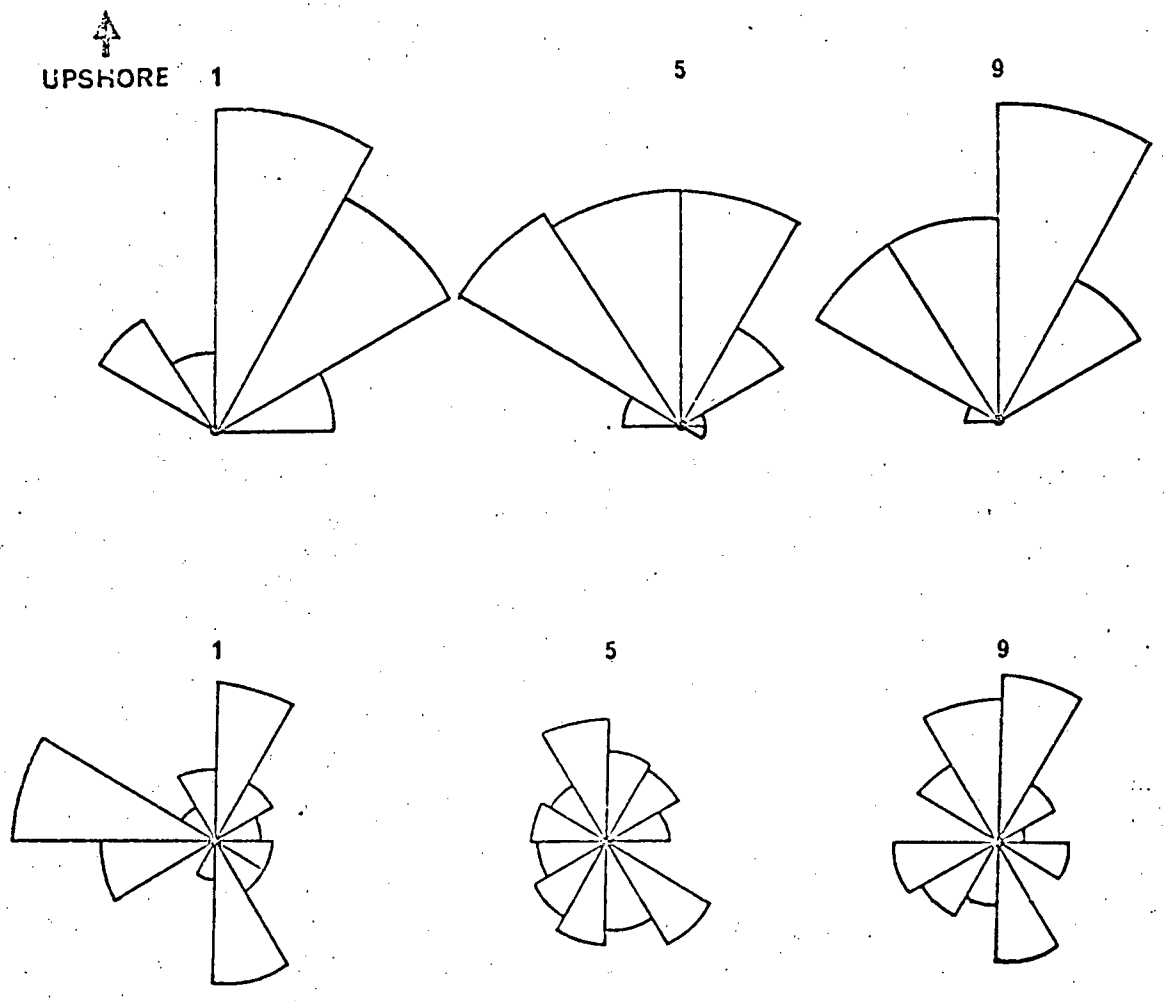


Fig. 2.13 : The direction of dispersal of marked juvenile L. a. knysnaensis 1, 5 and 9 days after release. Experimental animals upper figures, control animals lower.

(——— = 10 % of sample)

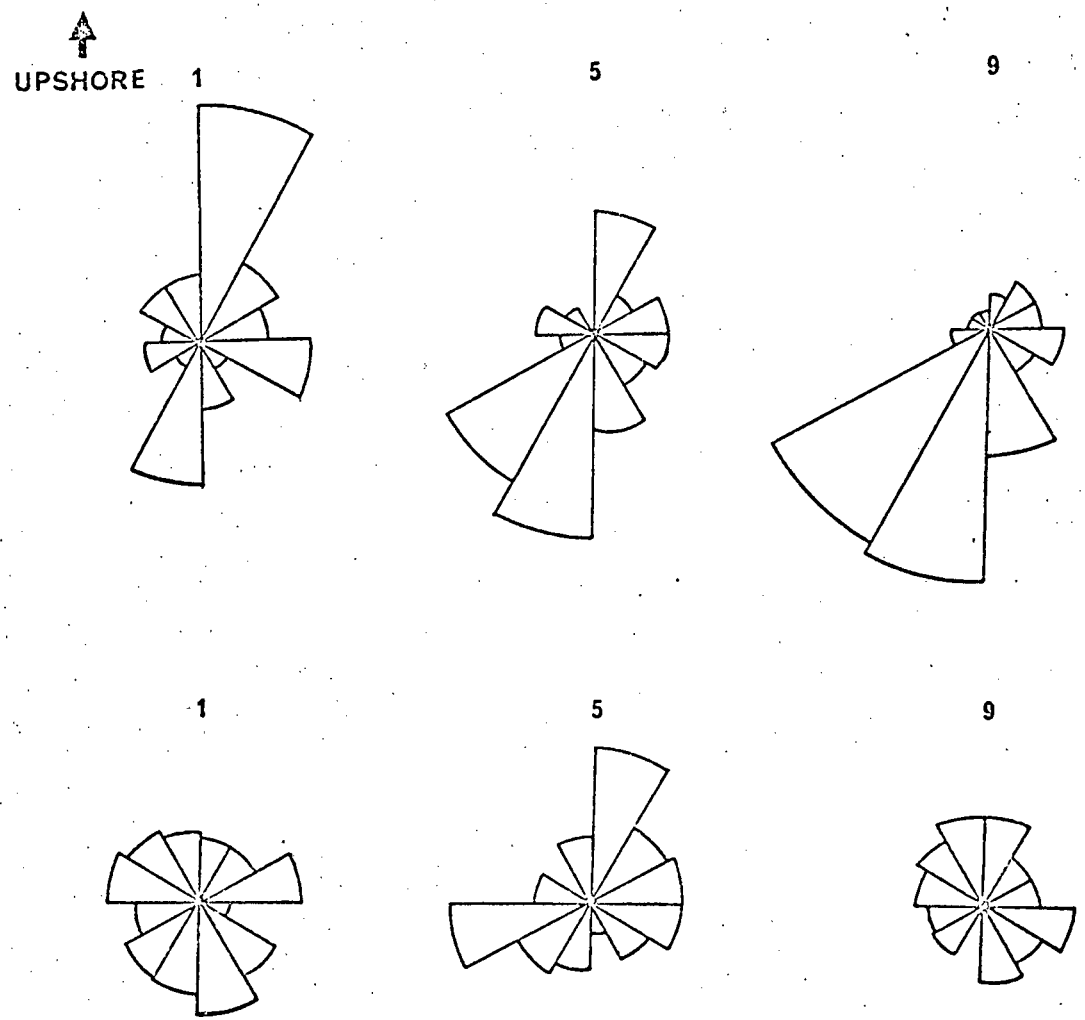


Fig. 2.14 : The direction of dispersal of marked adult L. a. knysnaensis 1, 5 and 9 days after release. Experimental animals upper figures, control animals lower.

(——— = 10 % of sample)

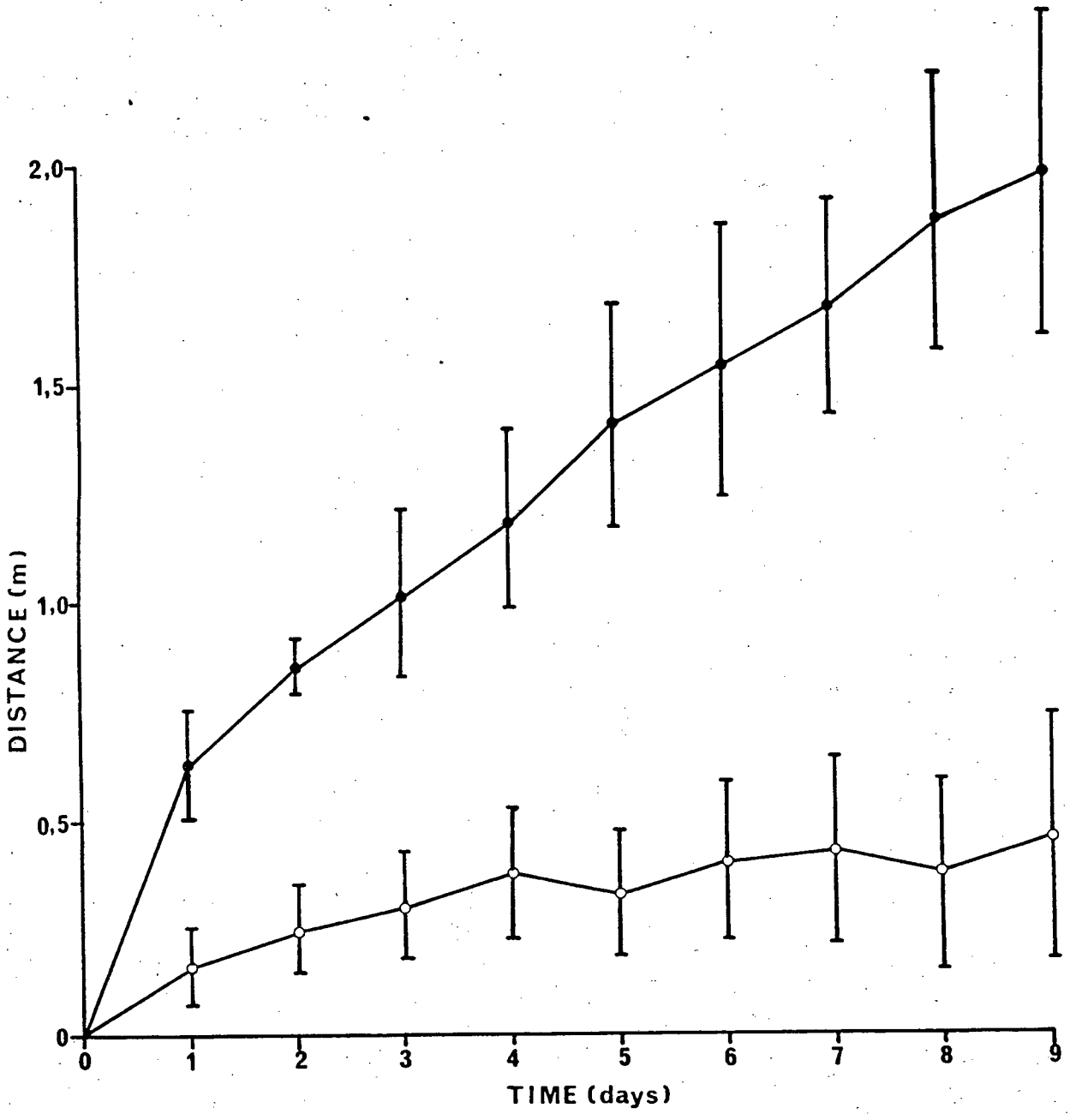


Fig. 2.15 : Mean distance (± S.D.) of marked samples of juvenile L. a. knysnaensis from the release point with time.

● = experimental O = control

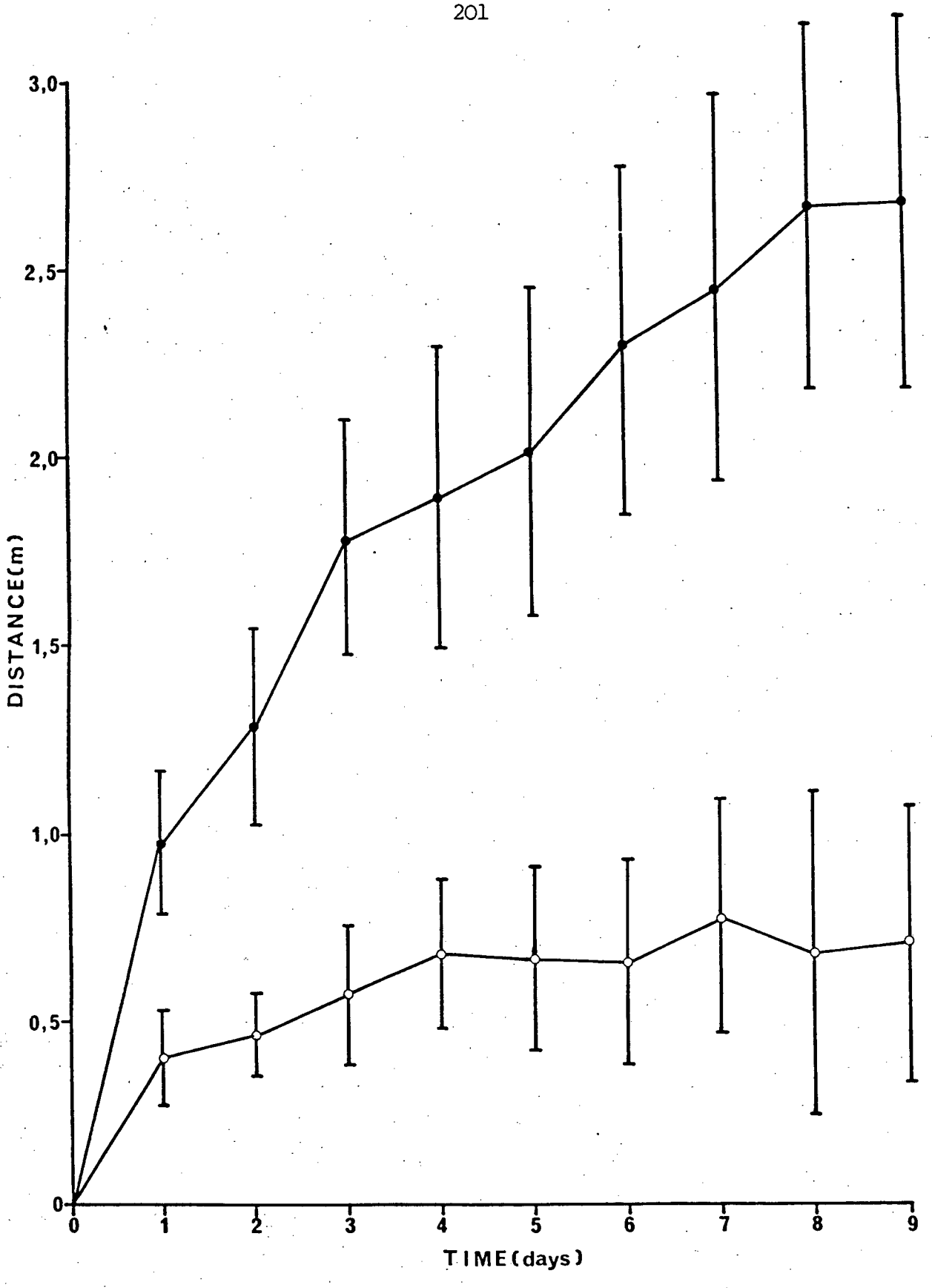


Fig. 2.16 : Mean distance (± S.D.) of marked samples of adult L. a. knysnaensis from the release point with time.

● = experimental O = control.

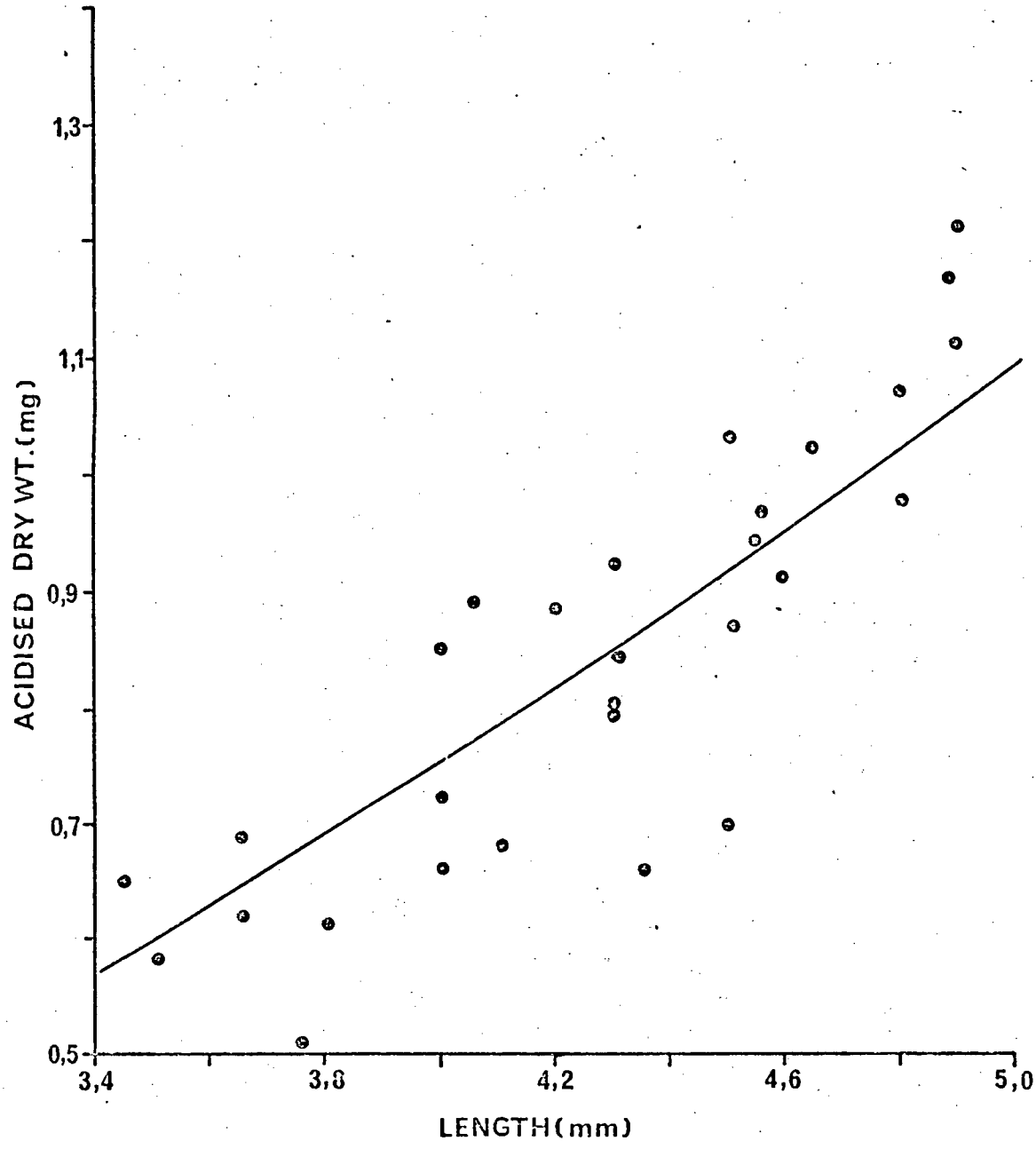


Fig. 2.17 : The relationship between shell length and acidised dry weight of juvenile L. a. knysnaensis tethered in the lower Littorina (zone A).

$$y = 0{,}0030 \times^{1{,}6875} \qquad (r = 0{,}75)$$

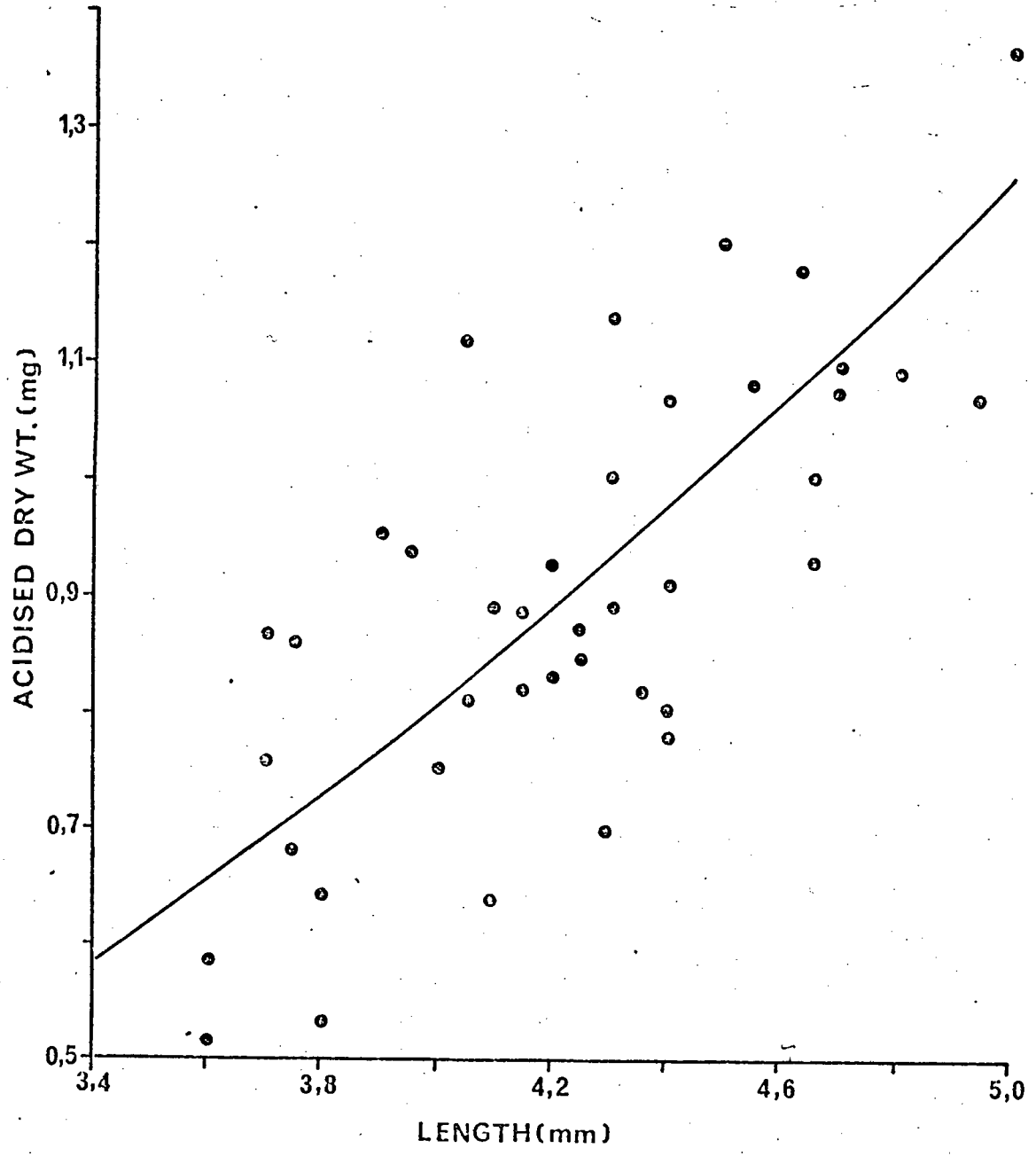


Fig. 2.18 : The relationship between shell length and acidised dry weight of juvenile L. a. knysnaensis tethered in the upper Littorina (zone C).

$$y = 0{,}0004 \times^{2{,}0341} \quad (r = 0{,}68)$$

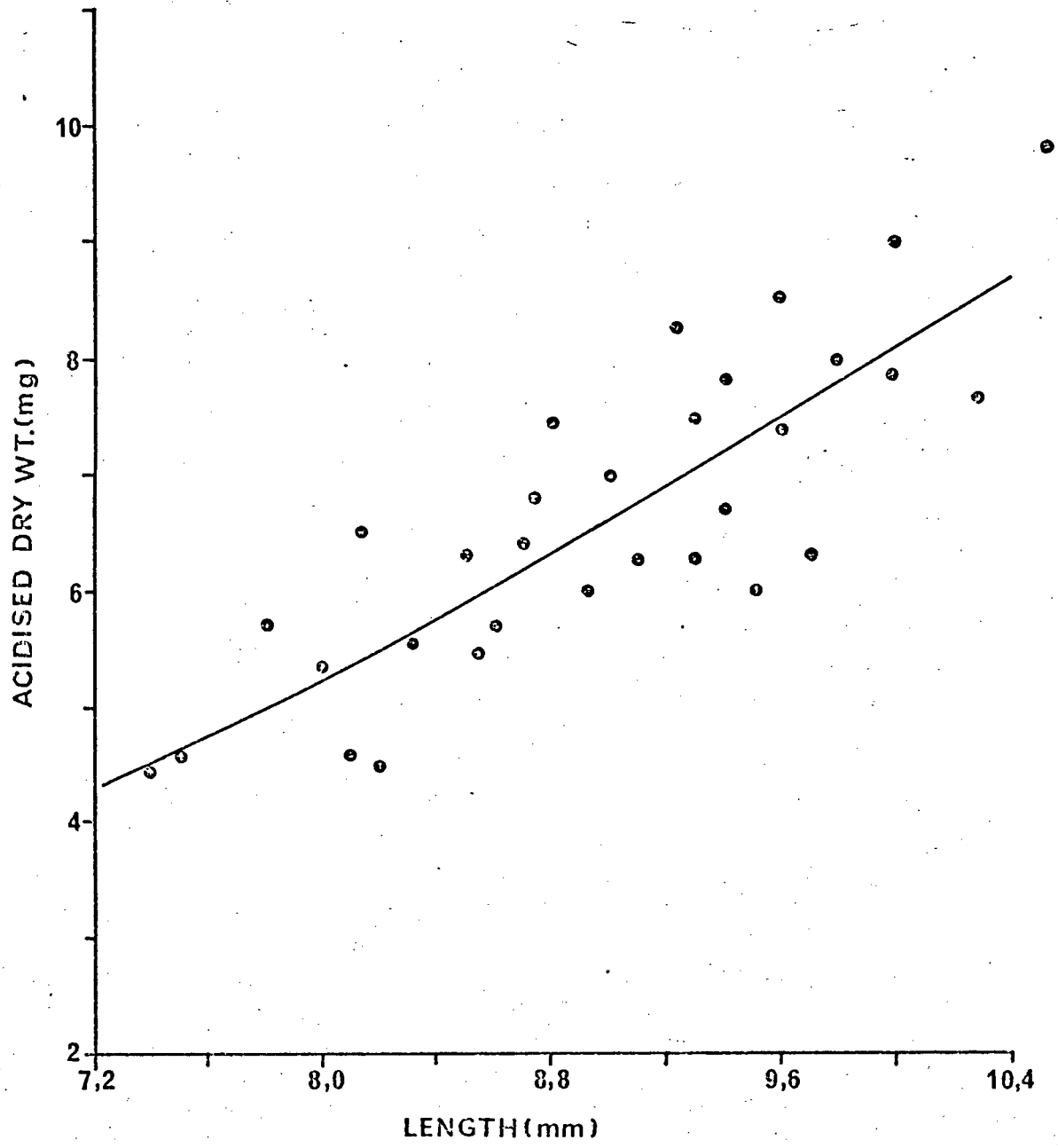


Fig. 2.19 : The relationship between shell length and acidised dry weight of adult L. a. knysnaensis tethered in the lower Littorina (zone A).

$$y = 0{,}00012\ x^{1{,}9482} \quad (r = 0{,}85)$$

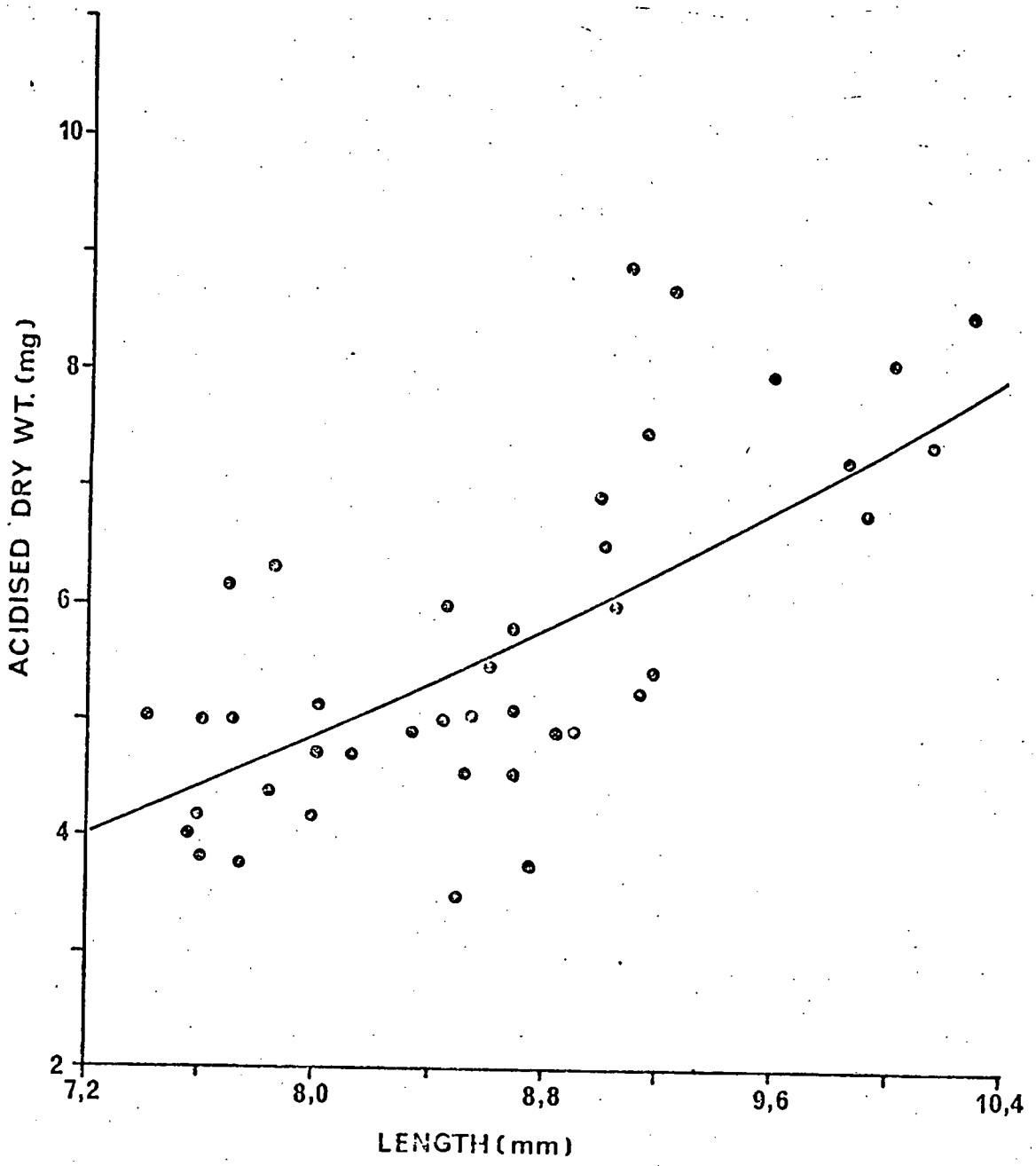


Fig. 2.20 : The relationship between shell length and acidised dry weight of adult L. a. knysnaensis tethered in the upper Littorina (zone C).

$$y = 0{,}00022\ x^{1{,}8417} \quad (r = 0{,}71)$$

(c) Tenacity and wave action

The relationship between snail size and tenacity is described by a steep power curve (fig. 2.21) revealing much greater tenacity in adult snails. This is supported by the fact that during the tethering experiments 17 juveniles were torn free of their tethers in zone A. No adults were lost in this way, nor were snails of either size class lost from zone C. Duplicate readings for several snails showed a high degree of consistency. Wave action was found to decrease in an upshore direction from zone A to zone C (Table 2.3).

TABLE 2.3 : WAVE EXPOSURE IN THE LITTORINA ZONE MEASURED USING A TURBULOMETER (MEAN OF THE 10 HIGHEST READINGS ± S.D.)

	Z O N E		
	Upper	Middle	Lower
Exposure (revs. $sec.^{-1}$)	3,20 ± 0,42	5,10 ± 0,88	6,10 ± 0,74

(d) Food availability

Productivity strips removed from the beach after one month during a pilot experiment yielded chlorophyll concentrations too low to be detected using this method. Even after a period of 90 days the values obtained were low indicating extremely slow settlement of microscopic primary producers in this zone. There is, however, a marked decrease in productivity moving upshore from zone A (Table 2.4).

TABLE 2.4 : CHLOROPHYLL a CONCENTRATION ON PRODUCTIVITY STRIPS EXPOSED IN THE LITTORINA ZONE FOR 90 DAYS (GIVEN AS MEANS OF 10 VALUES ± S.D.)

	Z O N E		
	Upper	Middle	Lower
Chlorophyll a concentration ($\mu g.cm^{-2}$)	0,30 ± 0,10	0,60 ± 0,10	1,20 ± 0,20

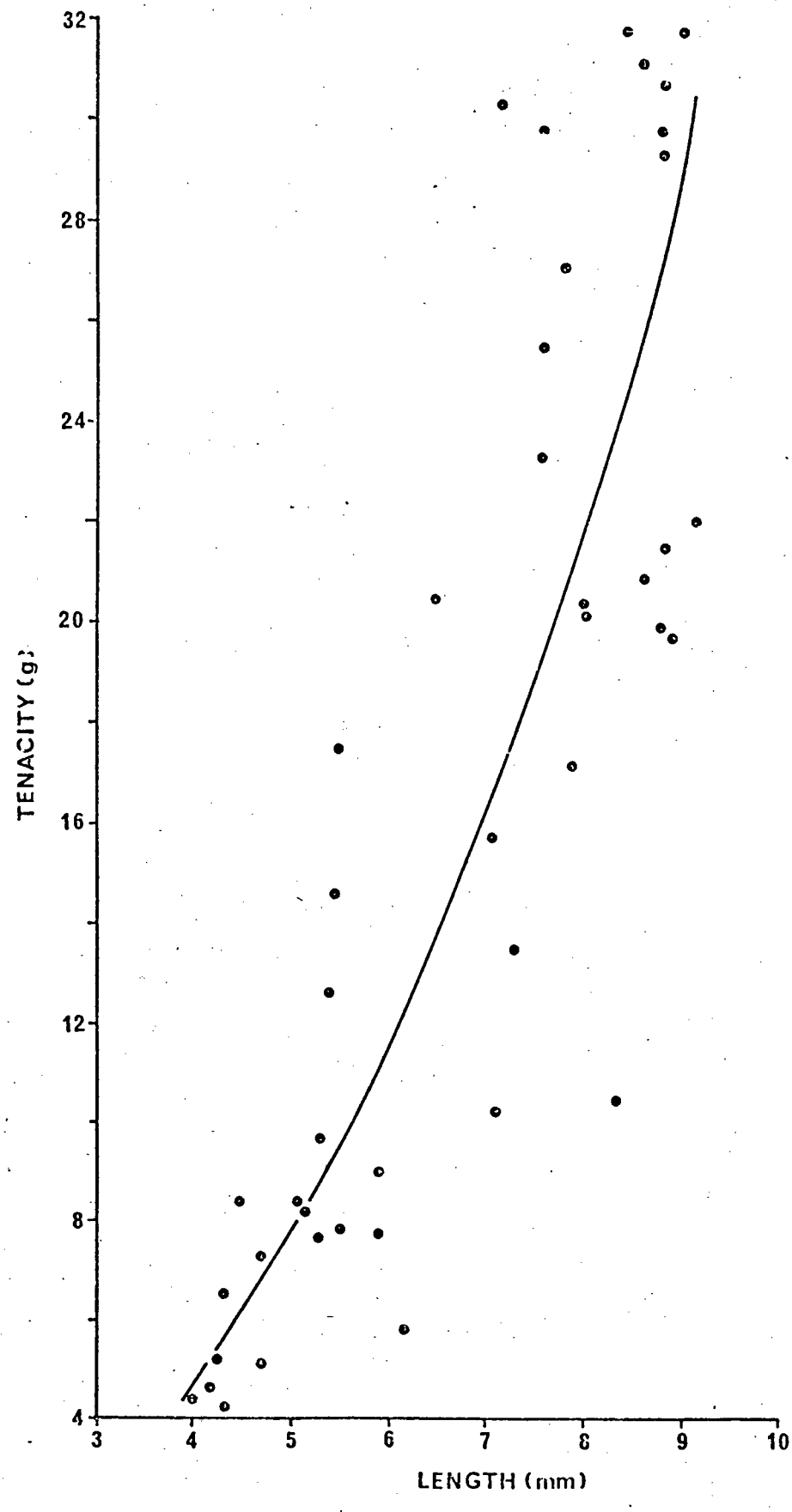


Fig. 2.21 : The relationship between shell length of L. a. knysnaensis and tenacity.

$$y = 35{,}71 \times^{2{,}228} \quad (r = 0{,}87)$$

3. Population dynamics

(a) Total population size

Recruitment was minimal and mortality high from November 1976 to March 1977 (Table 2.2) leading to a slow decline in total population (fig. 2.22). Numbers then increased dramatically during the winter recruitment period from May 1977 to September 1977. Settlement and total population decreased after October 1977 and then rose again with the onset of summer recruitment (January 1978). Changes in total population thus involve a slow decline in the period of low settlement followed by a rapid increase during periods of heavy settlement.

(b) Numerical distribution

Mean size versus density is plotted in fig. 2.23 for a typical month of light settlement and a month of heavy settlement. Size frequencies in each zone were unimodal and normally distributed during these months. Mean lengths were lower for October due to the presence of many juveniles but there is no apparent correlation between mean size and density. This is in contrast to the findings of Branch and Branch (unpublished data) for Littorina unifasciata.

Table 2.5 gives mean biomass, density, numbers and percentage of total population in each zone for February-March 1977 (light settlement period) and September 1977 - January 1978) (a period of heavy settlement).

TABLE 2.5 : BIOMASS, DENSITY AND PERCENTAGE OF TOTAL POPULATION IN ZONES A-C
(given as monthly means for periods of light and heavy settlement)

	LIGHT SETTLEMENT			HEAVY SETTLEMENT		
	ZONE			ZONE		
	A	B	C	A	B	C
Biomass ($g.m^{-2}$)	1,3172	0,3782	1,2802	0,3398	0,1997	0,1924
Number	1220,33	2835,33	7178,67	2527,50	11833,75	8909,50
Density $.m^{-2}$	139,79	47,54	280,86	289,52	97,52	348,57
% of total population	10,86	25,24	63,90	10,86	50,85	38,29

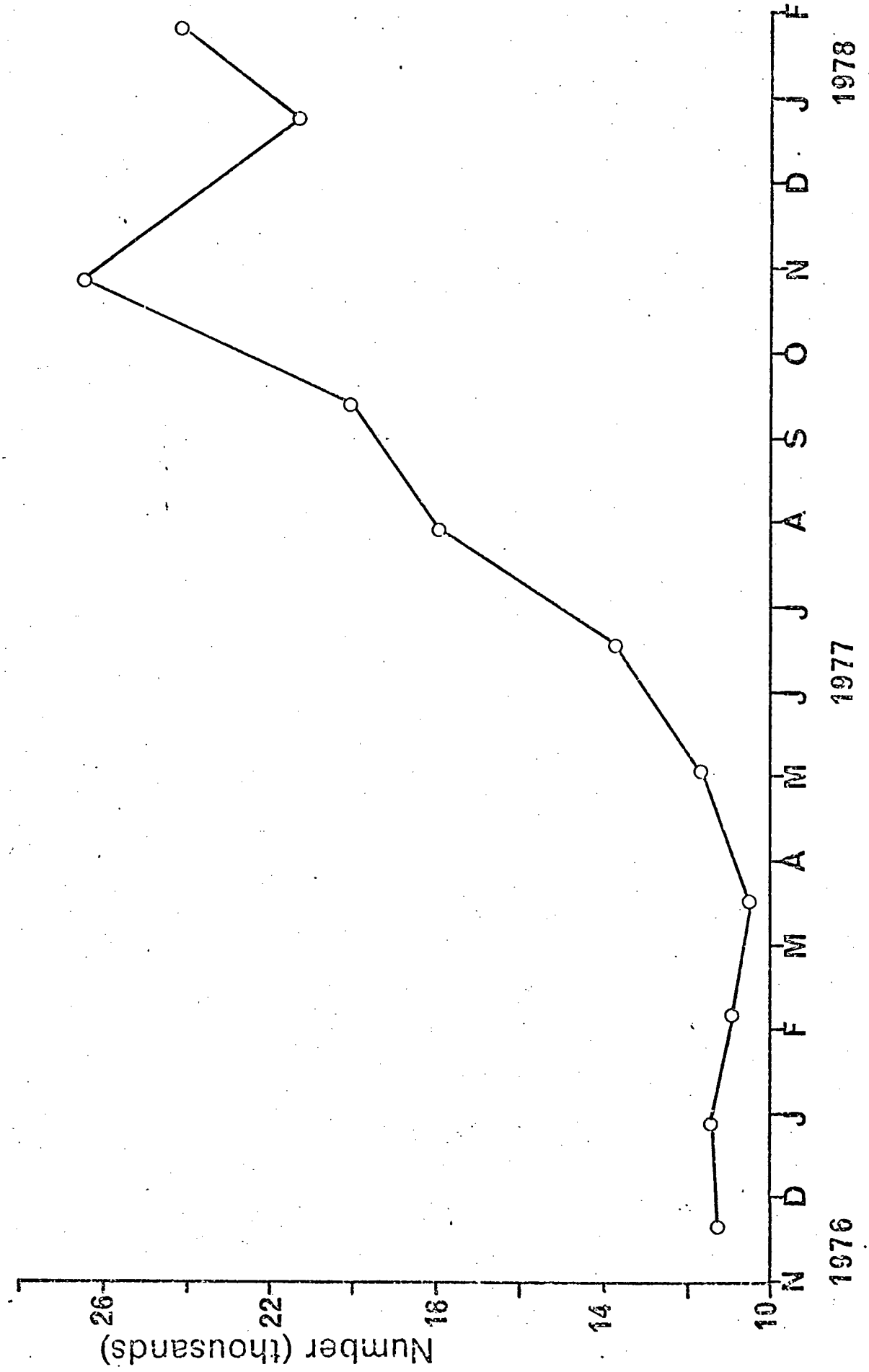


Fig. 2.22 : Total population size for Littorina africana knysnaensis at Dalebrook from November 1976 to January 1978 (derived at six-week intervals).

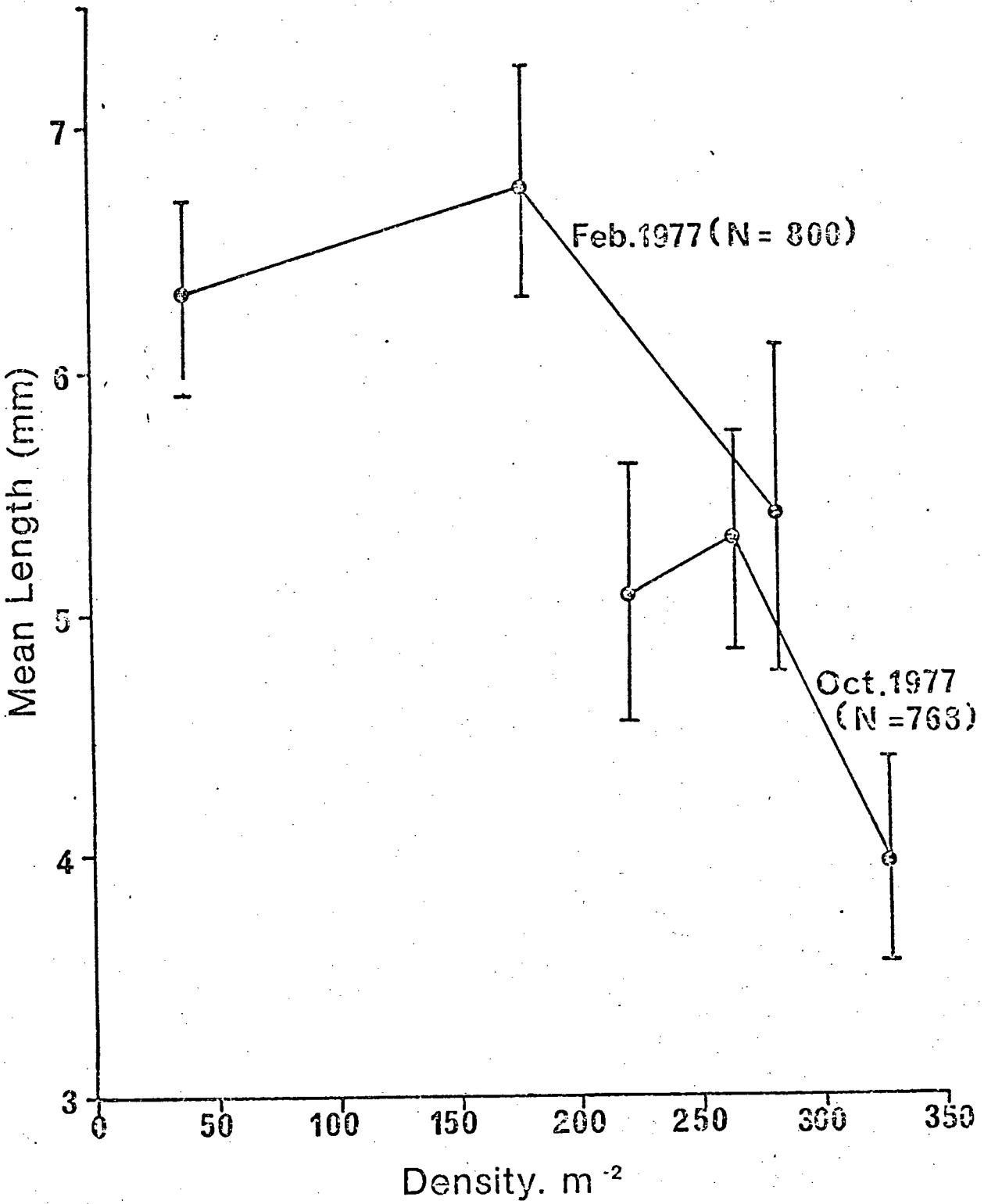


Fig. 2.23 : The relationship between mean length of Littorina africana knysnaensis and density in different zones for a month of light settlement (Feb. 1977) and of heavy settlement (October 1977). Mean lengths are given ± S.D. N indicates total sample size.

Density increased in all zones during heavy settlement but this was less marked in zone B as this sub-population extended into part of the zone which had been previously unoccupied. During months of light settlement zone C supported over 60 % of the total population. Because of the patterns of settlement described and migration of growing animals to the lower zones this value declined in subsequent months and a larger percentage of total population was found in zone B.

(c) Biomass

Mean biomass $.m^{-2}$ for light and heavy settlement periods, derived from size frequency data and seasonal length/weight regressions, is given for each zone in Table 2.5. Size frequency has a marked effect on biomass due to the exponential relationship between length and weight. Consequently there is no correlation between density and biomass, the latter being highest in zone A where mean size is greatest. Biomass $.m^{-2}$ decreased in all zones during heavy settlement despite an increase in density. This may be explained by patterns of size frequency during these periods. In February/March 1977 large numbers of older animals were present (figs. 2.10 - 2.12). Six months later however (September 1977-January 1978) many of these had died and were replaced by juveniles which made a far smaller contribution to biomass. This is reflected in a lowered mean size for each zone in months of light and heavy settlement (eg. fig. 2.23).

4. Growth Rates

(a) Long term growth

Mean growth rates for two consecutive periods of 7 months and percentage recovery at the end of each period are given in Table 2.6. Recovery was low due, in part at least, to loss of paint by an unknown percentage of the marked animals. Growth rates given are mean values over several seasons (see below) and decline with size. A lower growth rate for sample 1 than for sample 4 seems unusual but recovery for the former was very low and growth for sample 1 is probably underestimated. The growth rates observed are similar to average growth of L. planaxis given as 0,02 cm/month (=0,007 mm/day) by North (1954).

TABLE 2.6: MEAN GROWTH RATES AND PERCENTAGE RECOVERY AFTER 7 MONTHS FOR MARKED SAMPLES

Sample No.	Date marked	Number marked	mean length (mm ± S D)	final recovery date	Number re-covered	mean length (mm ± S D)	Δ L (mm)	Δ T (days)	Growth rate ($mm.day^{-1}$)	% recovered
1	20/12/77	250	2,47±0,24	22/7/78	8	5,11±0,84	2,64	214	0,0123	3,20
2	20/12/77	238	5,41±0,21	22/7/78	11	7,20±0,45	1,87	214	0,0084	4,62
3	20/12/77	207	8,44±0,30	22/7/78	18	9,40±0,51	0,96	214	0,0045	8,69
4	29/7/78	257	3,53±0,22	24/2/79	12	6,84±0,49	3,31	210	0,0158	4,66
5	29/7/78	220	5,49±0,29	24/2/79	9	7,12±0,59	1,63	210	0,0078	4,09
6	29/7/78	203	8,44±0,27	24/2/79	20	9,30±0,47	0,86	210	0,0041	9,85

Fig. 2.24 shows mean length for the six marked samples during two overlapping periods of seven months. Samples 4 and 5 overlap in their size ranges by the end of six months (December) illustrating how size dependent growth rates result in fusion of settlement cohorts in the size frequency histograms. Although growth rates for sample 1 were low they indicate that newly settled cohorts of 2-3 mm attain medium size (5-6 mm) within 7 months. Sample 5 may be considered as an extension of sample 1 showing that in a further 5 months (ie. a total of 1 year) animals reach about 7 mm.

Samples 3 and 6 show slow growth for large animals with a marked decline beyond 9 mm. Extrapolation from these rates suggests that 8-9 mm animals reach maximum size ($\geqslant$ 10 mm) only after at least a further year's growth.

We may conclude that newly settled animals reach above 7 mm after one year and that 8-9 mm animals reach maximum size after a further year. A longevity of approximately 2,5-3 years is thus indicated. The occurrence of occasional animals of 11-12 mm shows that a few individuals may live for a further 1 or possibly 2 years, growing at very slow rates although this may also be explained by particularly rapid initial growth of these animals.

The three sub-populations recognised thus consist primarily of animals of 2 years (zone A); 1-2 years (zone B) and $<$ 1 year old (zone C).

(b) Seasonal growth rates

Fig. 2.25 shows seasonal growth for small, medium and large animals. A decline in growth rate for larger animals is again evident. Growth was minimal for all three size classes during winter and rose again in spring. For small animals growth became maximal in summer. This was less marked for medium animals and for large animals growth was highest in spring and actually declined in summer.

5. Seasonal length-weight regressions

Regressions for autumn to summer are given in figs. 2.26-2.29. The results of t-tests used to compare the slopes and intercepts of the curves after log-log conversion are presented in Table 2.7.

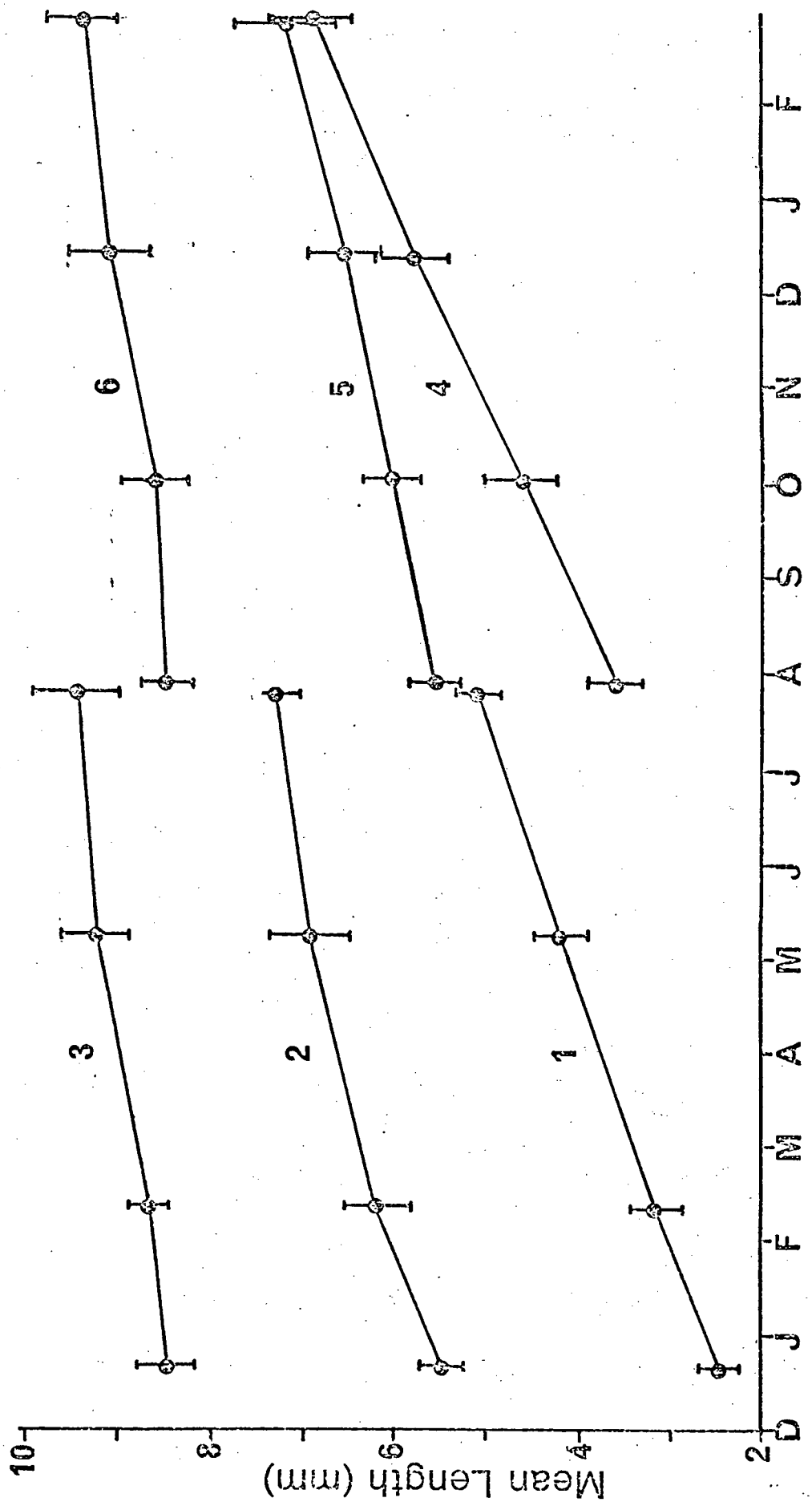


Fig. 2.24 : Mean length (± S.D.) of marked samples of Littorina africana knysnaensis for two consecutive periods of 7 months between December 1977 and February 1979.

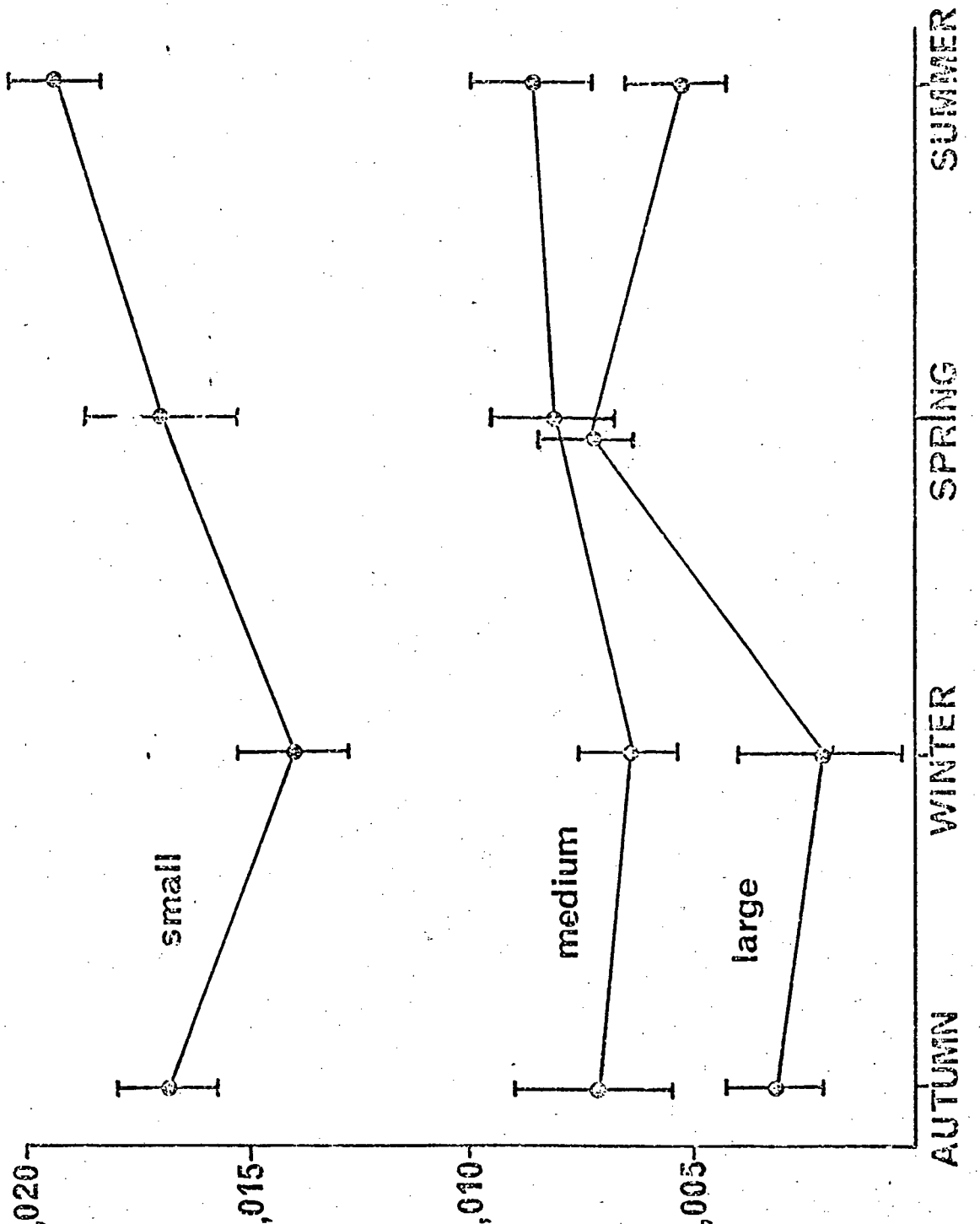


Fig. 2.25 : Seasonal growth rates for small (3-4 mm), medium (5-6 mm) and large (8-9 mm) Littorina africana knysnaensis. Each point indicates mean daily length increment (+ S.D.) derived over a period of 50-70 days for a sample of 100-150 animals.

TABLE 2.7 : VALUES OF t IN A COMPARISON OF SEASONAL LENGTH-ACIDISED DRY WEIGHT REGRESSIONS

(d.f. = 65 in tests involving autumn sample and 56 in all other tests;
* denotes a significant difference at 5% and ** at the 99% level)

		SLOPES			
		SUMMER	AUTUMN	WINTER	SPRING
INTERCEPTS	SUMMER		0,76	0,86	1,78*
	AUTUMN	0,15		0,42	3,36**
	WINTER	0,19	0,35		2,49**
	SPRING	0,47	0,42	0,59	

No significant differences were found between the intercepts of the four curves. Likewise the curves for summer (Jan. 1978), autumn (March 1977) and winter (June 1977) showed no significant differences in slope. Settlement rates and reproductive activity (examined by dissecting adult snails) were very low in March while animals of the June and January samples were spent having presumably contributed to the May/June and December settlements respectively. Reproductively active animals were however present before the December settlement in the September sample. The slope for this spring sample was significantly higher than for the remaining curves. This reflects the accumulation of reproductive products in the larger, mature animals of this sample (possibly reinforced by reduced growth during gonad maturation (Williams, E.E., 1964a) raising the distal end of the curve and thus increasing the slope. Significant differences in length-weight curves for breeding and non-breeding seasons have also been found for L. littorea by Grahame (1973).

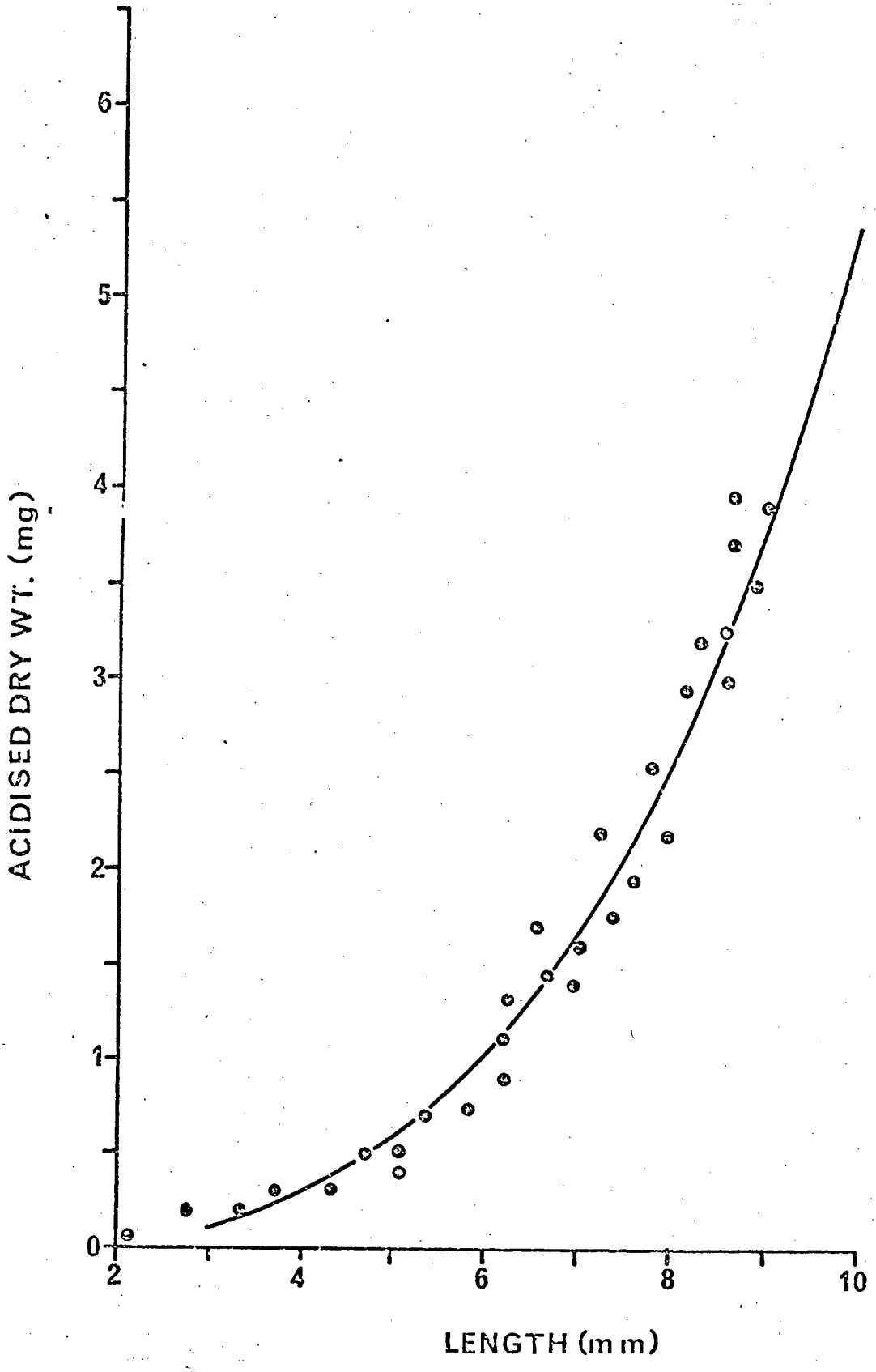


Fig. 2.26 : Length weight regression for L. a. knysnaensis collected in autumn (March 1977).

$$y = 0{,}00000347\ x^{3{,}1750} \quad (r = 0{,}98)$$

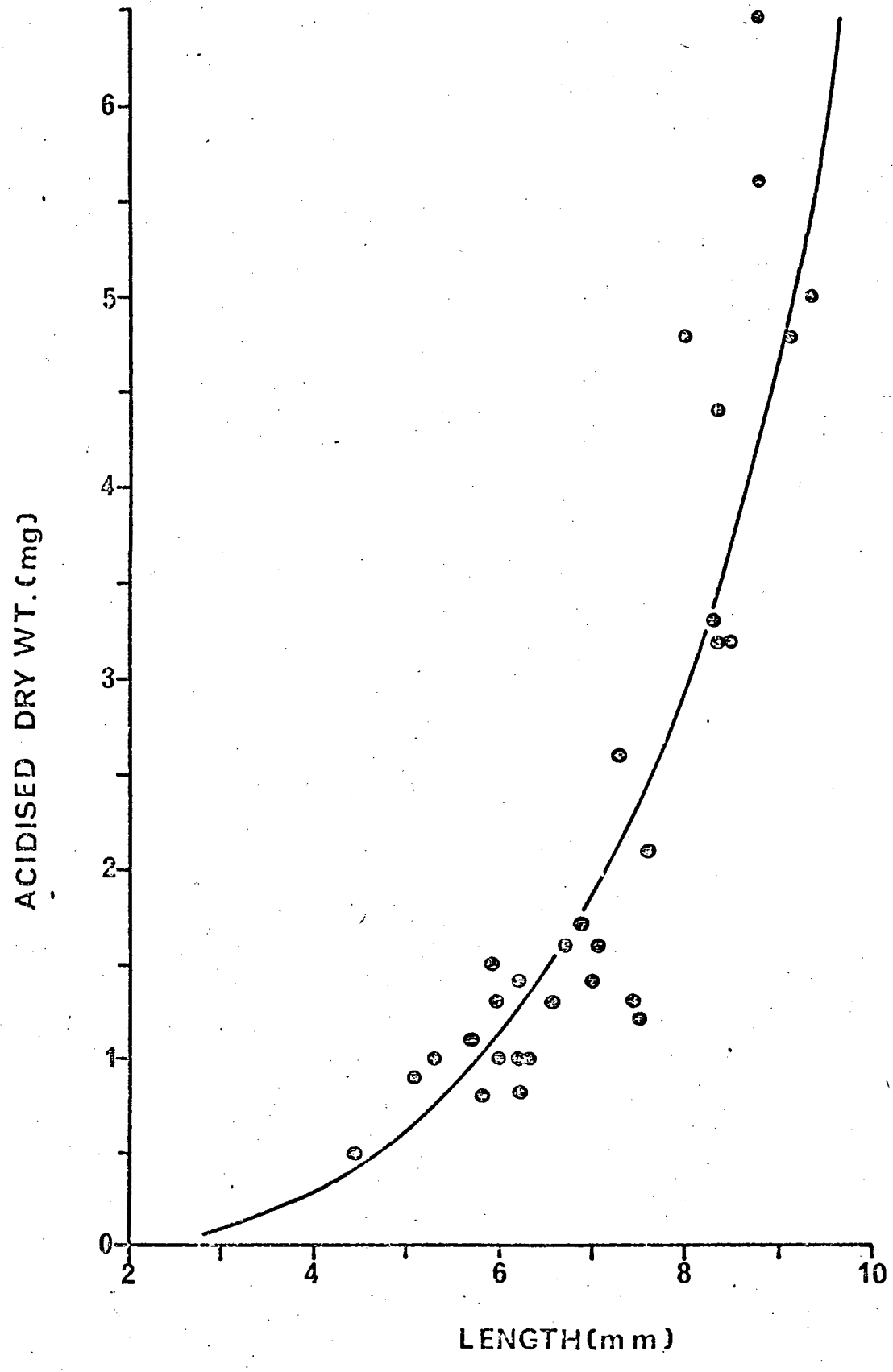


Fig. 2.27 : Length weight regression for L. a. knysnaensis collected in winter (June 1977).

$$y = 0{,}00000305\ x^{3{,}2993} \quad (r = 0{,}91)$$

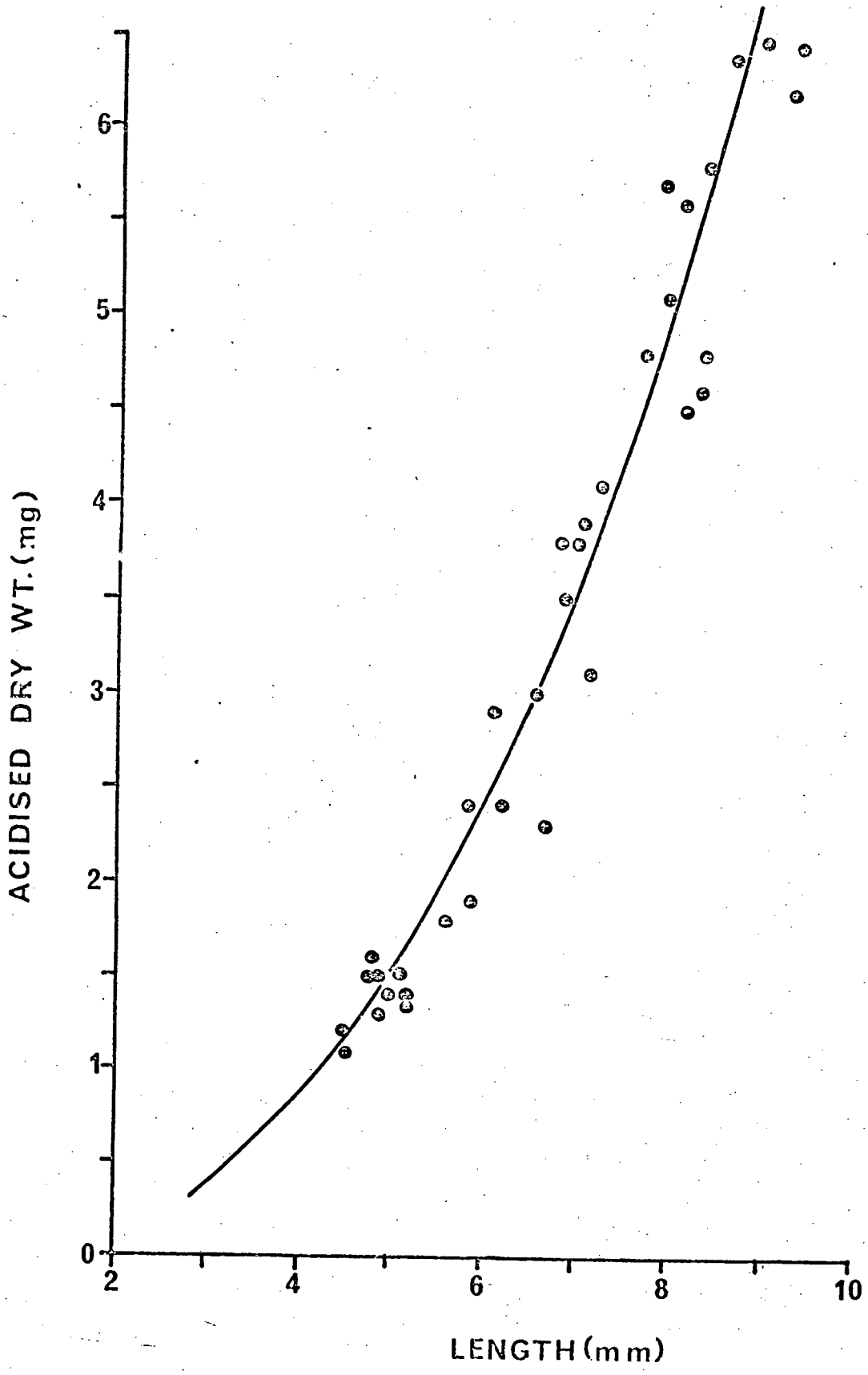


Fig. 2.28 : Length weight regression for L. a. knysnaensis collected in spring (September 1977).

$$y = 0{,}00002531 \times^{2{,}5380} \quad (r = 0{,}95)$$

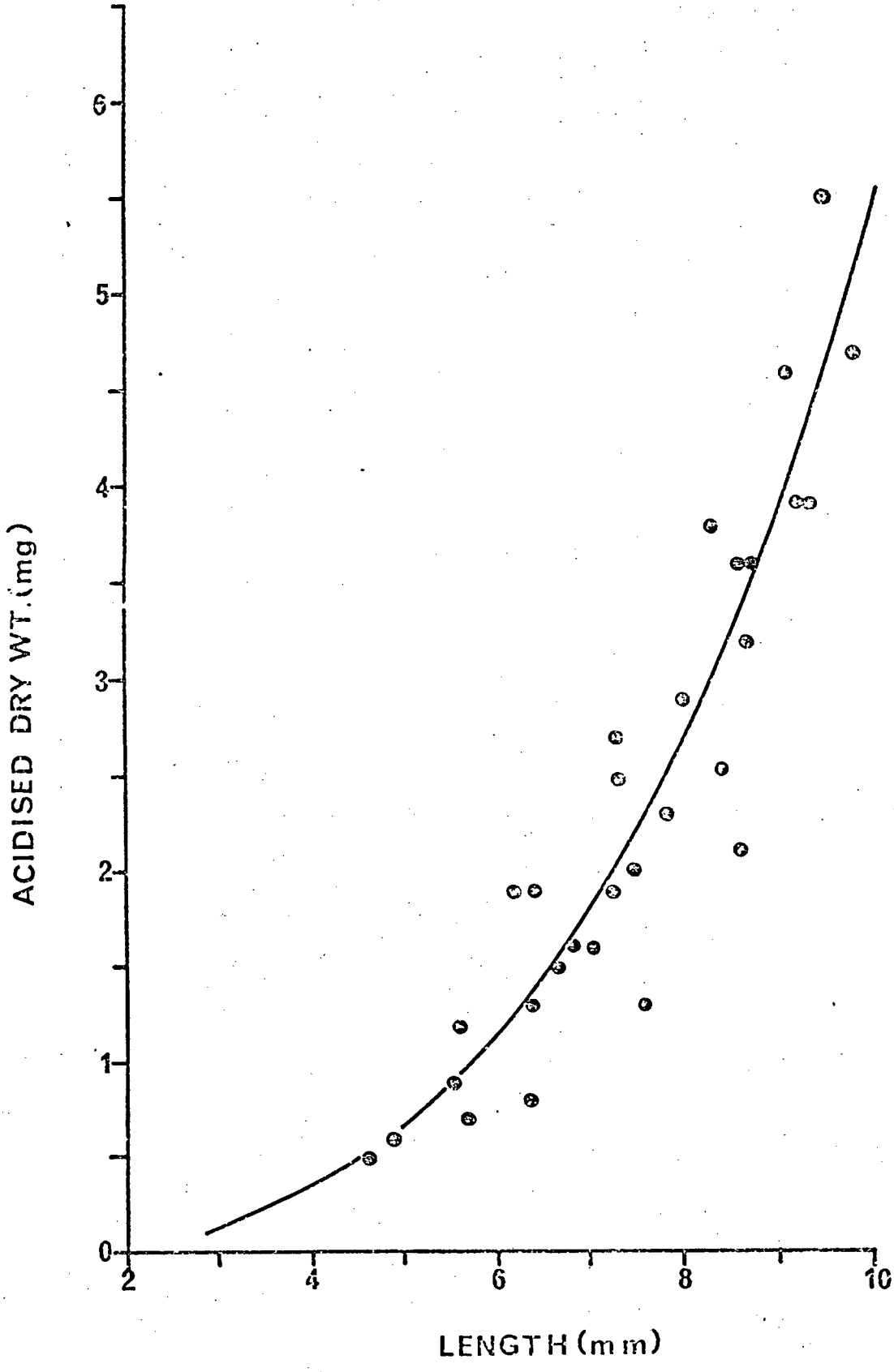


Fig. 2.29 : Length weight regression for L. a. knysnaensis collected in summer (January 1978).

$$y = 0{,}00000524 \times^{2{,}9955} \quad (r = 0{,}94)$$

DISCUSSION

Populations of Littorina africana knysnaensis in the Cape Peninsula exhibit marked size dependence in vertical zonation and continuous reproduction with seasonal peaks of settlement. The population studied remained roughly stable during the first months of sampling followed by a dramatic increase over the following eight months. In order to examine the cause and significance of these changes in the population patterns of zonation, population size and growth rates may now be considered in greater detail.

Size gradients

Size dependent zonation has been recorded for numerous other species of intertidal gastropods (eg. Lysaght, 1941; Bakker, 1959; Williams, E.E., 1964a; Bock and Johnson, 1967, Paine, 1969; Fish, 1972; Crapp, 1973; Lipkin and Safriel, 1971; Raffaelli and Hughes, 1978). This subject has been reviewed by Vermeij (1972) who recognises two basic patterns of size zonation. Type 1 applies to upper littoral fringe and high intertidal species and is characterised by an upshore increase in shell size. Type 2 relates to low and mid-intertidal species and entails a decrease in shell size farther up the shore. These gradients are considered to be maintained in response to patterns of post-settlement, pre-reproductive mortality. These are based primarily on physiological stress at the top of the shore (type 1) and intensified biotic interactions, including predation, lower down the shore (type 2). Heller (1976) has confirmed that a downshore increase in shell size in L. nigrolineata and L. rudis is a consequence of predation pressure but the case of L. a. knysnaensis is more complex.

Although it is a supralittoral fringe species L. a. knysnaensis shows a type 2 size gradient (fig. 2.9). There is no apparent correlation between density and size (fig. 2.23) though this has been observed for L. unifasciata (Branch and Branch, unpublished data). Instead the gradient shown appears to be due to separate size specific effects on juveniles and adults. The virtual absence of juveniles from zone A and their predominance in zone C are due to much higher rates of settlement at the top of the beach (Table 2.2). This may be an oversimplification as in this table the number of juveniles present is equated with settlement. It is possible that settlement is in fact random but rapidly followed by very high mortality in the lower zones. Nevertheless "successful" settlement (the number of juveniles growing to $>$ 1 mm) decreases down the shore and accounts for the

restriction of very small individuals to the top of the shore. At Dalebrook this effect is augmented by the local topography. A clear relationship between the size of available crevices and size distribution of L. rudis and L. neritoides has been demonstrated by Emson and Faller-Fritsch (1976) and Raffaelli and Hughes (1978). This relationship also exists at Dalebrook and appears to be effective through the restriction of juveniles to zones with narrow crevices. Maximum shelter is offered by the pitted boulders of zone C where small animals are most abundant. Crevice availability decreases in zone B and again in zone A as crevice width and mean animal size increase. Where narrow crevices do occur in zone A juveniles are common.

There are two reasons for assuming crevice dependence to be unrelated to desiccation effects. Firstly, although juvenile gastropods are often less resistant to desiccation than adults (eg. Davies, 1969; Coombs, 1973; Branch, 1975(c)) the resistance of L. a. knysnaensis is extremely high and its rate of water loss very low (Broekhuysen, 1941; Brown, 1960). This is augmented by withdrawal behind the operculum and attachment to the substratum by a mucous film (c.f. Vermeij, 1973) and even small individuals can survive in air for over a month (pers. obs.). Secondly not all beaches where this size gradient has been observed are characterised by greater crevice availability in the upper zones. Juveniles in the upper Littorina zone would therefore be subjected to a higher degree of desiccation without the benefit of high crevice availability.

However wave exposure decreases in an upshore direction (Table 2.3) and may be related to gradients in snail size because of the weaker tenacity of juveniles (fig. 2.21). For example 17 tethered juveniles were lost from Zone A while none were lost from zone C. Weight loss of juveniles tethered in zone A (figs. 2.17, 2.18) may therefore be caused by the interference of strong wave action with feeding. Narrow crevices offer protection from wave action allowing juveniles to survive where such shelter is available. Although juveniles transferred to zone A rapidly move upshore (figs. 2.13, 2.15) it was noticeable that the few animals which found suitable crevices remained there and did not migrate.

A higher resistance to wave action in small individuals of L. punctata has been suggested by Palant and Fishelson (1968) and observed for L. sitkana by Behrens (1972). Chow (1975) however found the reverse

for L. scutulata. Hylleberg and Christensen (1978) have shown a correlation between size gradients of L. littorea and wave exposure to be effective through increased tenacity in larger animals, as with L. a. knysnaensis.

The distribution of juvenile L. a. knysnaensis may therefore be explained by zone-dependent settlement, the lower zones being unsuitable for juveniles in terms of wave action. This does not however account for the size gradient of adults in zones A and B and their virtual absence from zone C. Zone C contains crevices suitable for all sizes of L. a. knysnaensis and offers very sheltered conditions. Removal of adults by either wind (Courtney, 1972) or wave action (Behrens, 1972; Walsby, 1977) is very unlikely. Instead this zonation is caused by downshore migration of older animals (figs. 2.14, 2.16). Thompson (1968) suggested that the emersion/submersion ratio is of direct importance in intertidal zonation but this was subsequently disproved for eight species of prosobranchs (Underwood, 1972a, b). A high resistance to desiccation and the ability to survive indefinitely in pools indicate that the duration of either emersion or submersion in different zones is unlikely to have a direct physiological influence on zonation of L. a. knysnaensis.

Underwood (1972b), following Smith and Newell (1955) has suggested that food availability in different zones may be important. The emersion/submersion ratio directly affects the time available for feeding, which only occurs under moist conditions. Although reduced feeding time at the top of the shore has been suggested as limiting the distribution of populations of limpets (Frank, 1965), this is compensated for in Littorina littorea by more rapid radular action in animals at the top of the shore (Newell et al, 1971). No data are available on feeding of L. a. knysnaensis but there are no macroalgae permanently present in its zone of distribution. Examination of faeces indicate that feeding is probably mainly on lichens, blue-green algae, diatoms and small encrusting algae (c.f. Branch, unpublished data; Castenholz, 1961; Dahl, 1965; Foster, 1965; Bock and Johnson, 1967; Nicotri, 1977). Littorina spp. are extremely tolerant to starvation (eg. Emerson and Duerr, 1967; Holland et al, 1975) but the primary productivity in zone C was so low (Table 2.4) as to result in significant weight loss in adults tethered in this zone after only one month (figs. 2.19, 2.20). Downshore migration of older animals thus appears to be in response to gradients of food

availability. As for L. littorea (Hylleberg and Christensen, 1978) movement towards areas of higher food levels is limited by size dependent tenacity (fig. 2.21) and increased wave action downshore (Table 2.3).

The direction of migration may be determined by light effects (Newell, 1958b; Charles, 1961a, b, c; Evans, 1965) or by wave movement after initiation by tidal rise and fall (Barkman, 1955; Alexander, 1960; Gendron, 1977). It seems however more likely to be simply a movement away from areas of low food availability to areas where food levels are high (eg. Underwood, 1977). Variations in microfloral standing crop in the three zones may thus account for downward migration of larger animals.

Numerical and Biomass distribution

During heavy settlement, recruitment increased in all three zones, but less markedly in zone C (Table 2.2). This effect was reinforced by inter-zone migration of growing animals resulting in different patterns of numerical distribution in the three zones during periods of light and heavy settlement. Percentage of total population and of juveniles of less than 4 mm at the bottom of the shore (zone A) remained fairly constant throughout the year at 10,86 and 6-7 % respectively (Tables 2.2, 2.5).

During light settlement (pre-May 1977) zone C contained 64 % of total population and, because of higher settlement rates than in the other zones, 87 % of the juveniles (Tables 2.2, 2.5). During heavy settlement (post-May 1977) the increase in recruitment was particularly great in zone B. Consequently the percentage of total juveniles in zone C was reduced to 57 %. Migration of growing animals from zone C down to zone B further diminished the percentage of the population in the former which dropped to 38 %, despite an increase in actual numbers (Table 2.5).

Size distribution has a marked influence on biomass, consequently biomass distribution did not follow density patterns but was highest in zone A where larger animals predominated (Table 2.5). Because of the different size distributions found during light and heavy settlement periods, biomass $.m^{-2}$, although still highest in zone A, was reduced

in all zones during heavy settlement, when there were few large animals present.

Changes in population size

Changes in the size of total population at Dalebrook fall into two phases : a period of limited fluctuation involving a gradual decline from November 1976 to March 1977; followed by a rapid increase beginning in May 1977 and leading to a 231 % rise in population over the following eight months (fig. 2.22). Population size varies due to the interplay of migration, mortality and settlement and drastic changes in one or more of these components are necessary to account for these fluctuations.

There are two main reasons for assuming migration effects to be limited. Firstly the population considered was chosen because of its physical isolation from other populations due to local topography. Secondly, although Hamilton (1978) found long-term movement of Littorina irrorata to be primarily parallel to the shore-line, his marked animals moved on average only 3,99 mm from their original position in 226 days. Migrations of Littorina spp. are more generally vertical and often markedly size dependent (eg. Gowanloch and Hayes, 1927; Lebour, 1945; Lambert and Farley, 1968; Chow, 1975; Williams and Ellis, 1975; Daguzan, 1976). Lateral movements are usually limited (Newell, 1958a; Underwood, 1977). In the present study marked animals were found in approximately the same area over long periods of time, as has only been reported by Colman (1933) and Moore (1937).

Mortality however was found to be higher in the phase of population decline (Table 2.2). Predation of L. a. knysnaensis at Dalebrook is limited to the whelk Thais dubia and only some half dozen of this species were observed in the Littorina zone during the entire sampling period. The cause of high mortality during this phase thus remains unclear. Population size began to increase with the onset of heavy settlement during winter (May/June, see figs. 2.10-2.12). This period of peak recruitment extended over several months, blending into the summer peak recruitment period (December/January). It must be stressed that the settlement rates recorded here are in fact rates of "successful" settlement. It is possible that settlement of larvae during the period of population decline was much heavier but followed by very rapid mortality so that relatively few animals grew to 1 mm or over. In this context it is

interesting that mortality of animals of greater than 1 mm actually declined during heavy settlement (Table 2.2).

Reproduction of L. a. knysnaensis was found to be continuous so that juveniles were present throughout the year. The rate of successful settlement however increased enormously after May 1977 resulting in a rise in population (Table 2.2, fig. 2.22). The period of heavy settlement (May 1977-January 1978) involved two peak periods, in winter (May/June) and in summer (December/January). A wide range of reproductive strategies exists among the Littorinidae and continuous reproduction by Littorina spp. has been recorded by Lysaght (1941) and Underwood, (1973) and, with seasonal maxima, by Lambert and Farley (1968) and Faller-Fritsch (1977). The method of reproduction of L. a. knysnaensis is unknown but examination of reproductively active specimens revealed that mature eggs are oblong and small, approximately 86,67µm x 83,33µm (c.f. maximum diameter of 80µm recorded by Underwood (1974) for mature ova of L. unifasciata, which has pelagic larvae). No evidence of viviparous brooding was found. Although these data are inconclusive the small egg size and absence of brooding or egg capsules suggest reproduction by means of pelagic larvae. Mileikovsky (1975) has reviewed the literature and found that most supra or upper littoral littorinids exhibit viviparous or pelagic development.

Organisms at the top of the shore tend to show reduced genetic variability due to strong selection for resistance to physical extremes (Newell, 1979). Viviparous reproduction of species such as Littorina rudis leads to low rates of gene flow and consequently extreme phenotypic variability in separate populations (Faller-Fritsch, 1977). Pelagic dispersal of L. a. knysnaensis is again implied by the absence of such local variability in this species which shows a gradual phenotypic cline along 2000 miles of coastline (Hughes, 1979).

For slow moving forms such as Littorina spp. pelagic larvae represent the most efficient means of dispersal and increasing gene flow. However settlement of pelagic larvae is strongly influenced by offshore wind, current and sea temperature conditions. Recruitment may therefore be locally unpredictable and may be unsuccessful for prolonged periods (Underwood, 1975a, b). This may account for low settlement and recruitment prior to March 1977.

Growth rates

Cohorts of L. a. knysnaensis are recruited at 2-3 mm and during the entire sampling period no individuals of less than 1 mm were found. It is unlikely that larvae settle at more than 1 mm. As the 1-2 mm size class is never abundant (figs. 2.10 - 2.12) settlement must therefore be followed by rapid growth to 2 mm. For example Berry (1961) measured growth from 0,75 mm to 3,00 mm in 6-7 weeks for the viviparous species L. saxatilis. Smith and Newell (1955) found that the smallest specimens of L. littorea on the shore were 2,5 mm while post-metamorphic larvae in the plankton never exceeded 0,5 mm. On this basis they postulated subtidal settlement and development of larvae. This was thought to be followed by continuous recruitment by migration from this zone. At Dalebrook however careful checks were carried out further down the shore, in the mid-balanoid zone, in the course of a simultaneous study on Oxystele variegata populations. Although O. variegata of less than 2 mm were recorded no specimens of L. a. knysnaensis were found below the normal zone of distribution. Vertical migration of juveniles from the subtidal zone may thus be excluded.

After settlement growth decreases with size, being particularly rapid for small animals (fig. 2.25). Preliminary examinations indicated that L. a. knysnaensis attains sexual maturity at $\geqslant$ 5 mm and lifespan appears to be 2,5 - 3 years with a few individuals living for 4 or 5 years, as has been found for L. obesa and L. scabra (Comfort, 1957). Newly settled animals grow to 6-7 mm in their first year and approach 10 mm after three years.

Superimposed on these growth patterns are seasonal variations in growth rate for any given size class (fig. 2.25). Growth was minimal in winter for all three size classes examined. Maximum rates however occurred in summer for small and medium animals and in spring for large animals. This is in contrast to the findings of Regis (1969) that growth of Monodonta spp. is maximal in summer and minimal in spring. Seasonal growth rates and different seasonal maxima for the size classes are likely to be related to food availability in the three zones occupied. In Chapter 5 it was found that physical conditions became optimal for macroalgal growth towards summer but that this occurred earlier in the year in the lowest zones. A similar effect on the microflora would

account for growth rates of the largest animals (lowest zone) peaking earlier than rates for smaller animals. The difference between spring and summer growth rates is less marked for medium sized animals (middle zone) than for small animals at the top of the shore (fig. 2.25). This mirrors macroalgal growth patterns on the rest of the beach and may reflect a temporally progressive upshore extension of optimum conditions for microflora in the sub-zones of the Littorina zone.

The population of L. a. knysnaensis examined showed wide fluctuations in numbers which may be accounted for by the effects of offshore conditions on the success of settlement of pelagic larvae. Post-settlement growth is very rapid but settlement and survival of juveniles is zone dependent. Intense wave action in the lower zones excludes juveniles due to their weak tenacity and they exhibit reduced body weight if forced to remain in these zones. Juveniles are consequently restricted to the upper zones. Food availability is very low on the upper shore however and adults in these zones show weight loss. The increased tenacity of growing animals allows them to migrate downshore to exploit the greater food resources available. Restriction of juveniles by physical conditions to zones which are biologically sub-optimal for adults and subsequent migration as the animals grow result in a marked vertical size gradient which has profound effects on the density and biomass distribution of the species.

SUMMARY

1. Littorina africana knysnaensis exhibits a marked decrease in shell length up the shore in the Cape Peninsula. This is caused by preferential settlement in the higher zones (augmented at Dalebrook by the absence of crevices suitable for juveniles lower down) and age dependent downshore migration of adults.

2. Density is highest at the top of the shore (around 348 animals $.m^{-2}$) but there is no apparent relationship between mean size or biomass $.m^{-2}$ and density.

3. Total population declined slowly from November 1976 to March 1977 due to reduced settlement and high mortality. From May 1977 to January 1978 recruitment rates were higher and mortality decreased resulting in a 231 % rise in population over 8 months.

4. Reproduction appears to involve pelagic larvae and is continuous throughout the year. Settlement success is very variable and is probably influenced by offshore conditions. There are however peak periods of settlement in winter (May/June) and summer (December/January).

5. Growth after settlement decreases with size. Juveniles attain sexual maturity at approximately 5 mm and grow to 6-7 mm in their first year. Maximum size of roughly 10 mm is attained after three years. Normal lifespan is 2,5-3 years.

6. Growth for all size classes is at a minimum in winter. For small and medium animals maximum rates occur in summer; for large animals they occur in spring. This is thought to reflect the seasonality of microalgal standing crop in the different zones occupied by these size classes.

CHAPTER 7 : POPULATION DYNAMICS AND SIZE DEPENDENT ZONATION OF OXYSTELE VARIEGATA (ANTON) (GASTROPODA : PROSOBRANCHIA).

INTRODUCTION

There are four species of Oxystele found on the east coast of South Africa of which only three extend as far west as the Cape Peninsula. O. sinensis reaches the limits of its distribution in False Bay while O. tigrina and O. variegata occur along the west coast to South West Africa. O. sinensis and O. tigrina are low and mid balanoid species respectively while O. variegata (the smallest of the three) is common throughout the balanoid zone.

At Dalebrook, in False Bay, O. variegata is extremely abundant and is likely to form an important element of the energetics of the intertidal community. In order to assess the importance of this species as a grazer, data are required on the dimensions and dynamics of the population. These include details of seasonal changes in the population including changes in both its size, zonation and age structure. They also include estimates of life expectancy, growth and mortality rates.

Like many other intertidal gastropods O. variegata exhibits a distinct size gradient up the shore (c.f. Bakker, 1959; Paine, 1969; Vermeij, 1972; Coombs, 1973; Bertness, 1977). As in the case of Littorina africana knysnaensis (Chap. 6) this gradient is the reverse of Vermeij's (1972) model as mean size increases in an upshore direction. Vertical size and density gradients imply that the impact of the species as a herbivore will depend on the zone considered. An examination of the underlying causes of this size gradient is therefore critical to an understanding of the structuring of this population and thus of the community as a whole.

The size distribution observed was considered to be due to upshore migration of growing animals, after settlement in the lowest zones, and was examined in terms of exclusion of juveniles from the upper shore and exclusion of adults from the lower shore (ie. the cause of migration). Broekhuysen (1941) and Brown (1960) have demonstrated a correlation between the zonation of intertidal gastropods and their resistance to desiccation. Juvenile gastropods however often exhibit a lower tolerance to desiccation

than adults (eg. Davies, 1969; Coombs, 1973; Branch, 1975(c)) and this may be expected to influence juvenile zonation. Field observations suggested the importance of predation in the lower balanoid as a possible cause of upshore migration.

METHODS

1. Population size and structure

O. variegata increases in size up the shore so that the population is dominated by different size classes in the lower, middle and upper balanoid zone. These zones were numbered 1-3 respectively. The animals occupying each zone were considered separately and are referred to as "subpopulations" for convenience. Each sub-population was examined at six-weekly intervals for a 15 month period (Sept. 1976 - Dec. 1977) in zone 1 and for 13 months (Nov. 1976 - Dec. 1977) in zones 2 and 3. Collections of 250 - 400 animals from each zone were measured and then replaced on the beach during each sampling session. The measure of body size used was maximum shell diameter which is highly correlated with acidised body weight ($y = 0{,}00001445 \times ^{3{,}5980}$: $r^2 = 0{,}98$).

The total area occupied by the species was 420 m^2, composed of 182 m^2 in zone 1; 149 m^2 in zone 2 and 89 m^2 in zone 3. Localized conditions necessitated a different method of quantifying the population in each zone.

Zone 1 Transects were laid down across the beach. These were 1m wide and varied in length so that a suitable number of animals was collected.

Zone 2 A fixed quadrat of 2,50m x 2,10m was established. All animals within the area were collected, particular care being taken to search the tests of dead barnacles (Tetraclita serrata) for small animals. Towards the end of the sampling period the quadrat was enlarged to incorporate sufficient animals.

Zone 3 Distribution within this zone was so clumped that population size could only be derived by directly counting all snails in the zone. Total population was calculated by adding this value to those for population in zones 1 and 2, obtained by multiplying density $.m^{-2}$ by the area of each zone.

2. Maintenance of size gradients

(a) Migration

Migration experiments were carried out as described in Chap. 6, 100 marked adults (> 16mm) being transferred from the upper to the lower balanoid and the reverse for 100 marked juveniles (< 10mm). Separate samples of 100 animals of each size class were replaced in their original zones as controls.

(b) Caging experiments

As in the case of L. a. knysnaensis it was necessary to determine whether adult and juvenile animals had a reduced ecological efficiency when forced to remain in the zones which they do not normally inhabit. Tethering experiments proved to be inappropriate due to interference by predators (see below). Consequently two stainless steel cages (20 cm x 20 cm, 10 cm high) covered with 2mm nylon mesh were fixed in the lower balanoid and two in the upper balanoid, using fibre-glass matting and resin. Fifteen adults were placed in each cage for two weeks after which the cages were relocated within the same zones and the experiment repeated using 20 juveniles in each cage. The bodies of adult animals were extracted from their shells, after severing the columella muscle and shell diameter/dry body weight regressions derived for the upper and lower balanoid samples. Student's t-tests were used to compare the slopes and intercepts of the two samples. In the case of juveniles, mortality was checked daily for five days.

In order to relate the results of caging experiments to field conditions an estimate of food availability in each zone was obtained using polyethylene productivity strips as described in Chap. 6. These yielded a measure of primary productivity, in terms of chlorophyll a concentration, over a period of 90 days.

(c) Resistance to desiccation

The tolerance of adult and juvenile O. variegata to desiccation was investigated by examining :

(i) The relationship between body size and operculum size. This is likely to influence the rate of water loss strongly as loss through the shell is generally minimal (eg. Branch, 1975 (c)). Body volume was measured by water displacement using a burette, and the maximum diameter of the operculum measured for a range of animal sizes.

(ii) Rates of water loss during desiccation and the relationship between body size and the lethal limits of water loss. These were determined by placing 60 animals of a range of sizes in a desiccator over silica gel at 20°C. Each animal was weighed at intervals and mortality checked over a period of 171 hours. The criterion of death used was failure to respond to tactile stimulation of the foot. Additional animals were desiccated for 4 hours to provide supplementary data on water loss over this period. At the conclusion of the experiment shell-free dry body weight was derived for each snail by extracting the body from the shell. The operculum was excluded from body weight. Rates of water loss were subsequently expressed as percentage of dry body weight following Brown (1960). This method equates weight loss with water loss and does not allow for weight loss due to respiration. This was however minimal as the animals remained completely quiescent during desiccation experiments.

(iii) Survival times at low humidities.
Mortality rates of adults ($>$ 16mm diameter) and juveniles ($<$ 10mm) at various humidities were obtained by placing 10 animals of each size class into each of 6 desiccators. Each desiccator contained a solution of sulphuric acid of known concentration (measured gravimetrically) in the lower compartment. Equilibrium humidity at 20°C over each solution was obtained from the Handbook of Chemistry and Physics (1975) and mortality checked at intervals as above.

(d) Predation

Attacks on O. variegata by the whelk Burnupena delalandii occur only under submerged conditions (ie. only in pools or as the tide rises) so that observations on natural rates of predation are extremely difficult. This is augmented by the fact that the shells of animals which have been killed are rapidly washed away. However comparative rates

may be obtained for the upper and lower balanoid by tethering animals to the beach (see Chap. 6) in which case the empty shells remain tethered. Samples of 50 adult O. variegata were tethered at the top and the bottom of the balanoid zone and mortality checked daily for 9 days. The experiment was carried out on two separate occasions.

3. Growth rates

O. variegata does not exhibit obvious growth rings (c.f. Paine, 1969) and the difficulties of marking individual trochids for long periods have been pointed out by Darby (1964). Growth rates were therefore derived from cohort analysis of the size frequency data. Histograms of size numbers versus size were examined using the polymodal graph analysis described by Harding (1949) and Cassie (1954). The graphically derived means and standard deviations for each cohort identified were then entered into the computer programme NORMSEP (Hasselblad, 1966). This programme examines the raw histogram data and fits a normal distribution to the cohorts based on the means and standard deviations provided. NORMSEP then employs a χ^2 test for goodness of fit between the observed frequencies and the sum of the normal distributions calculated by the programme (ie. predicted frequencies). These tests showed no significant differences in all cases ($P > 0,05$). The computer programme NHIST written by Mike Ripp of the Department of Environmental Studies at the University of Cape Town, was then used to plot the original histograms with superimposed normal distribution curves for each cohort. Due to limitations of this programme the 21 and 22 mm size classes are omitted from the figures for zone 3. This involved only 9 out of 3281 animals measured in this zone during sampling and the curves given are based on data in which they are included.

RESULTS

1. Size Distribution and Settlement

Patterns of settlement, indicated by the occurrence of small animals, may be most easily understood by considering firstly data summed for the entire population and then size distribution in each zone separately.

The population as a whole (fig. 2.30) exhibited a mode of size distribution around 13-14 mm except during heavy settlement. Reproduction appears to be continuous as small individuals were present throughout the year, but there was a marked peak of settlement in February 1977 when a very large cohort of juveniles appeared (cohort B on fig. 2.30). Mean size for this cohort gradually increased due to growth and by September 1977 it had merged completely with the older cohort (cohort A) already present which probably already comprised several fused cohorts. Smaller juvenile cohorts (C and D) appeared in March 1977 and October 1977 but these cohorts were both very small (fig. 2.30) and it is evident that there is one period of large-scale settlement during the year in February/March.

Size frequency histograms with superimposed curves for normal distribution are provided for each six-weekly sample for the three zones considered in figs. 2.31-2.33. Each zone contained a bi- or trimodally distributed population dominated by one particular size class with new cohorts appearing during settlement.

Zone 1 (fig. 2.31) was dominated by the 14-15mm size class from September 1976, when settlement began. In September 1976 individuals from a previous settlement were present as a 4mm cohort which merged with the older cohorts by May 1977. During February 1977 heavy settlement rates had resulted in the numerical domination of the population by a cohort of 3-4mm (ie. cohort B on fig. 2.30). These animals grew progressively and attained 14-15mm in October 1977. Smaller scale settlement also occurred in July and October 1977. The apparent reduction and subsequent increase of the larger cohort between February and May 1977 is an artifact caused by the temporary but massive preponderance of juveniles during this period.

Zone 2 (fig. 2.32) was also dominated by the 14-15mm size class. Again settlement occurred in December 1976 - February 1977 but a much smaller number of juveniles were involved. This recruitment period appeared to be extended (due largely to migration of juveniles from zone 1, see below) and merged with the winter peak of settlement in May/June 1977. A smaller spring settlement also occurred in October 1977.

Fig. 2.30 : Size frequency distribution for the entire population of Oxystele variegata at Dalebrook at six weekly intervals from November 1976 to December 1977. Normal distribution curves for each component cohort were plotted using the computer programme NHIST. Data on the last three size classes are omitted due to limitations of this programme but the numbers involved were small and curves were calculated from data including all animals (see text). Frequencies were calculated from density measures and data from figs. 2.31 - 2.33. N indicates total population size and identified cohorts are labelled A-D.

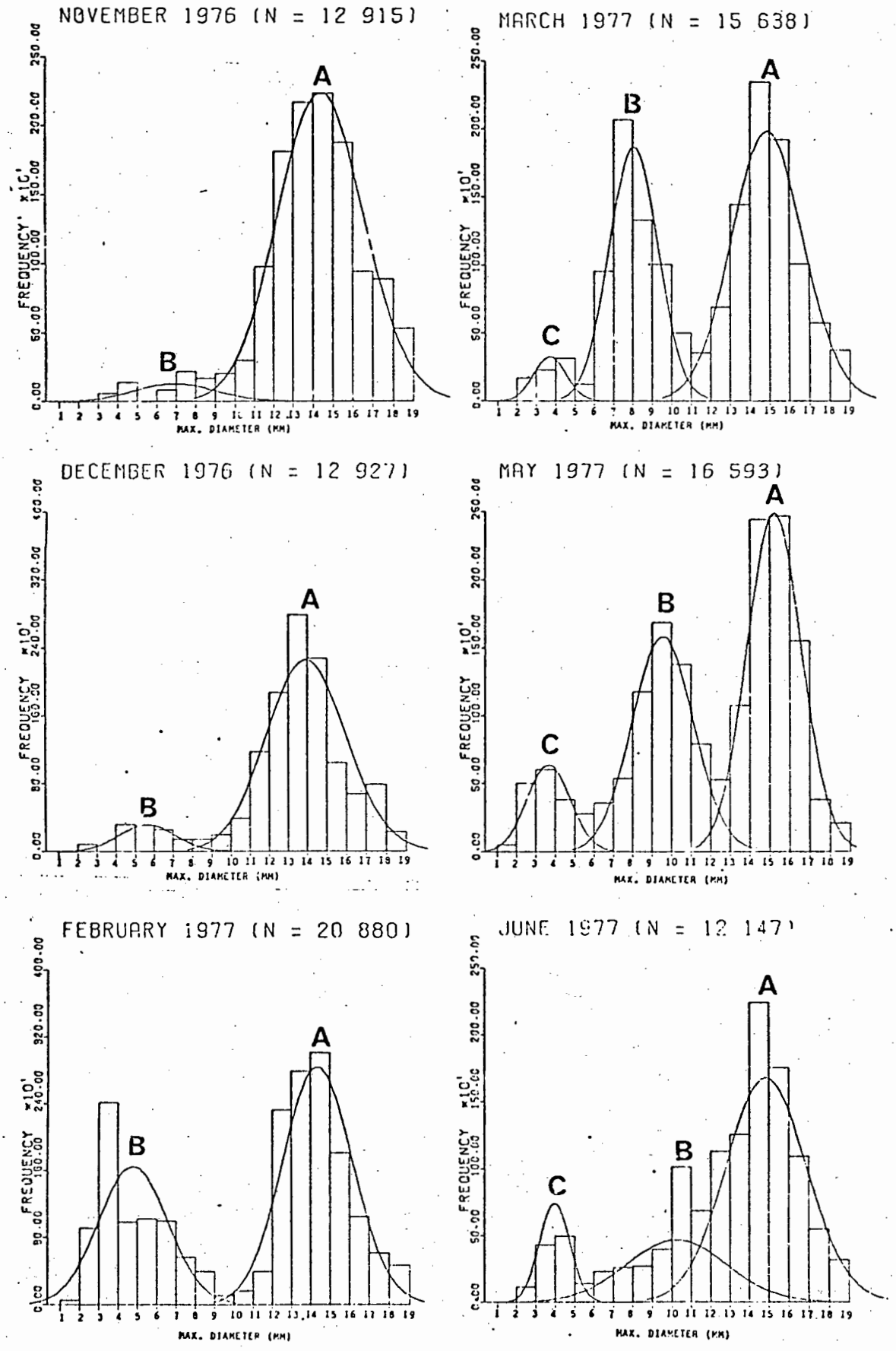

NOVEMBER 1976 (N = 12 915)
MARCH 1977 (N = 15 638)
DECEMBER 1976 (N = 12 927)
MAY 1977 (N = 16 593)
FEBRUARY 1977 (N = 20 880)
JUNE 1977 (N = 12 147)
FREQUENCY *10'
MAX. DIAMETER (MM)
A
B
C

Fig. 2.30

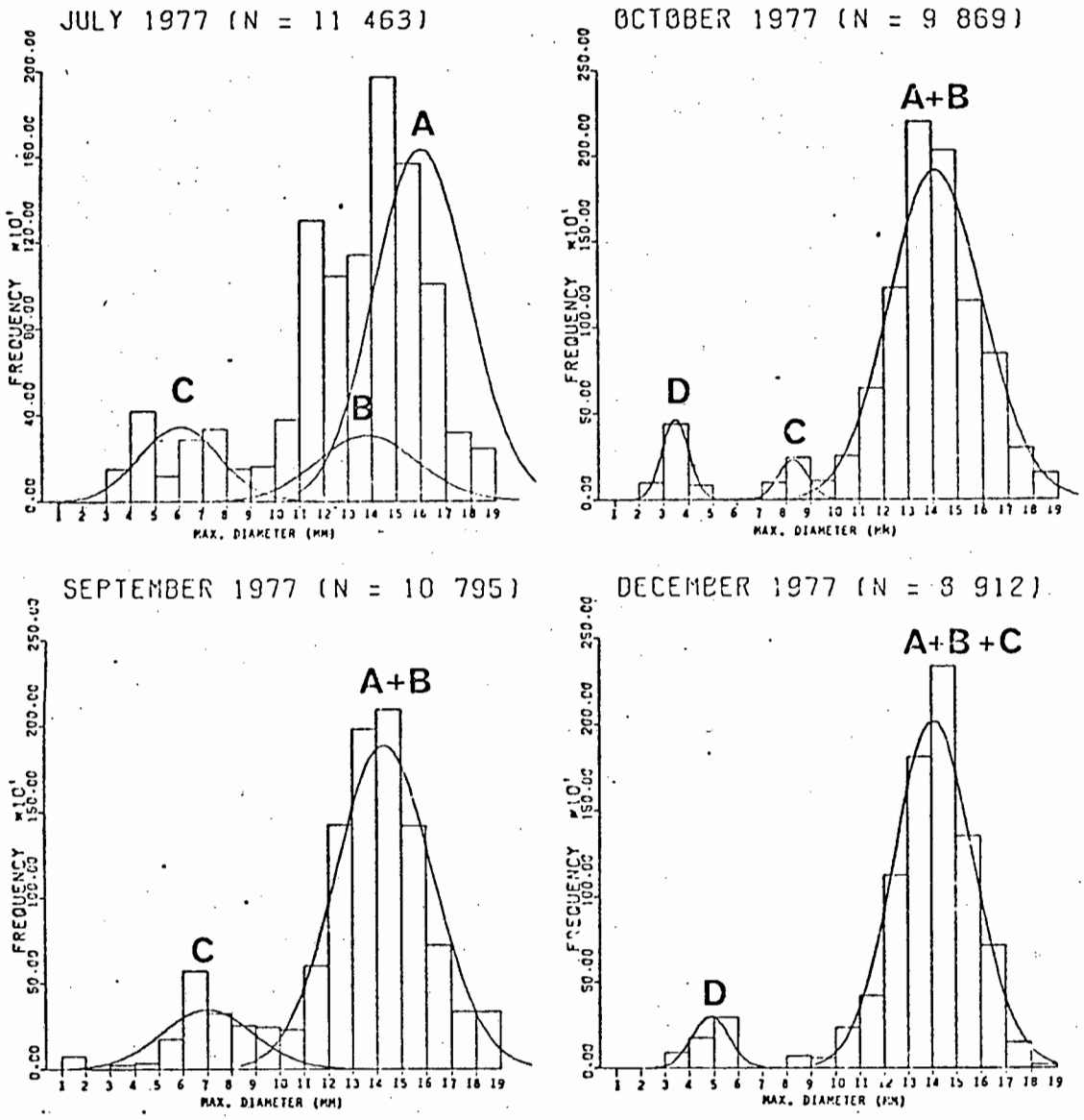


Fig. 2.30 (cont'd)

Fig. 2.31 : Size frequency distribution for Oxystele variegata in zone 1 at Dalebrook at six-weekly intervals from September 1976 to December 1977. Normal distribution curves plotted for each cohort as in fig. 2.30. N indicates sample size.

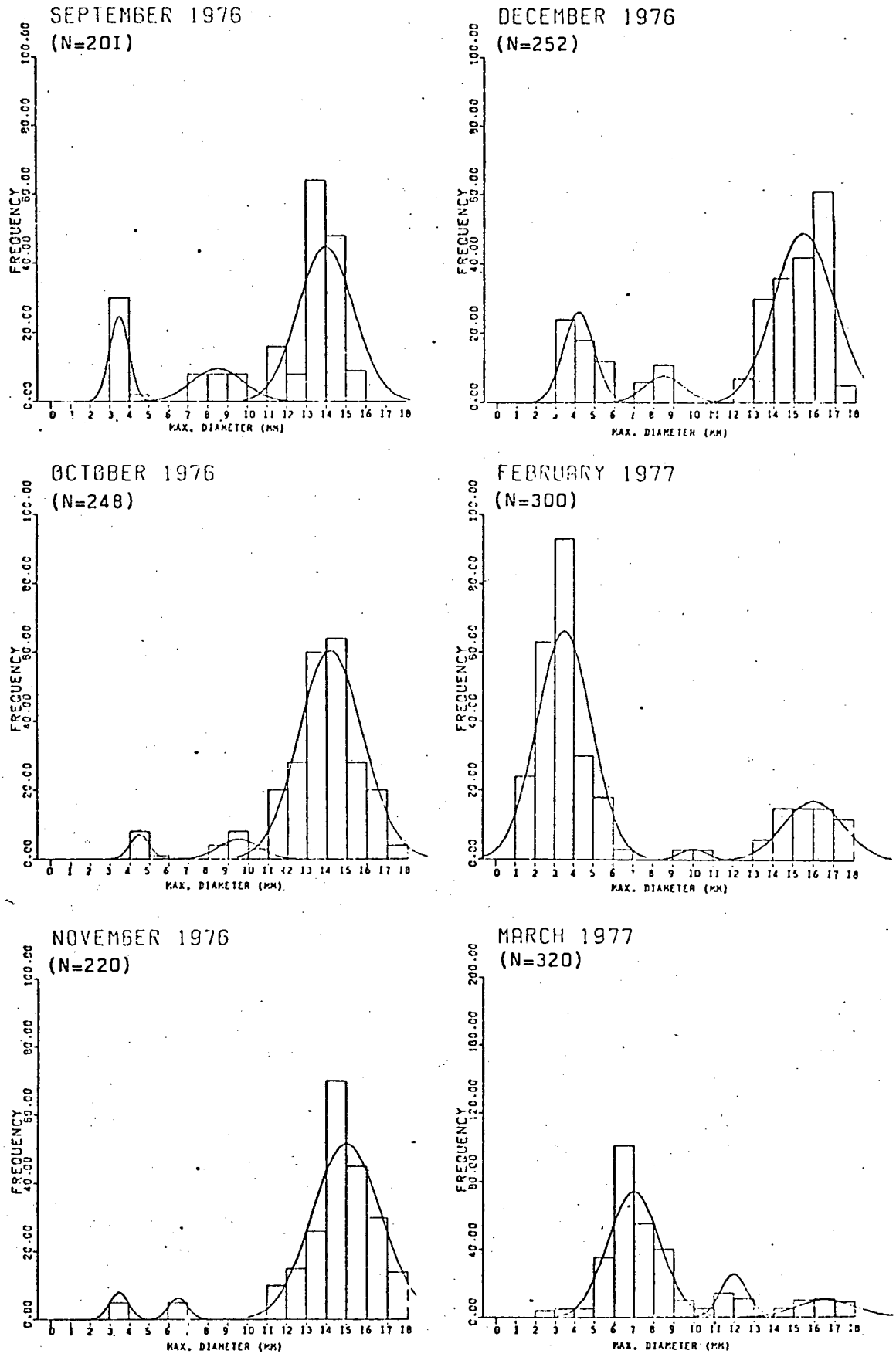

SEPTEMBER 1976
(N=201)
DECEMBER 1976
(N=252)
OCTOBER 1976
(N=248)
FEBRUARY 1977
(N=300)
NOVEMBER 1976
(N=220)
MARCH 1977
(N=320)
FREQUENCY
MAX. DIAMETER (MM)

Fig. 2.31

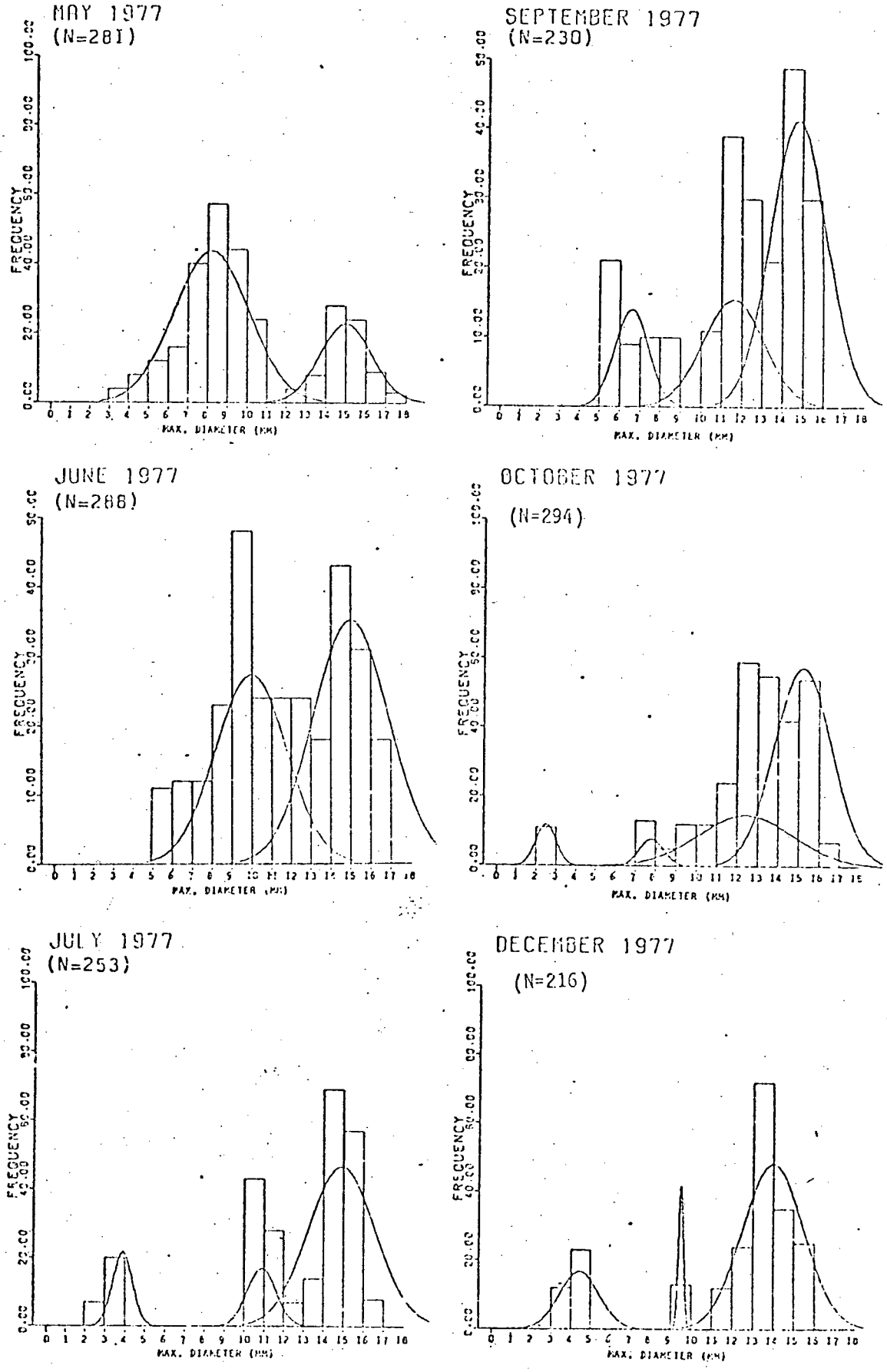


Fig. 2.31 (Cont'd)

Fig. 2.32 : Size frequency distribution for Oxystele variegata in zone 2 at Dalebrook at six-weekly intervals from November 1976 to December 1977. Normal distribution curves plotted for each cohort as in fig. 2.30.
N indicates sample size.

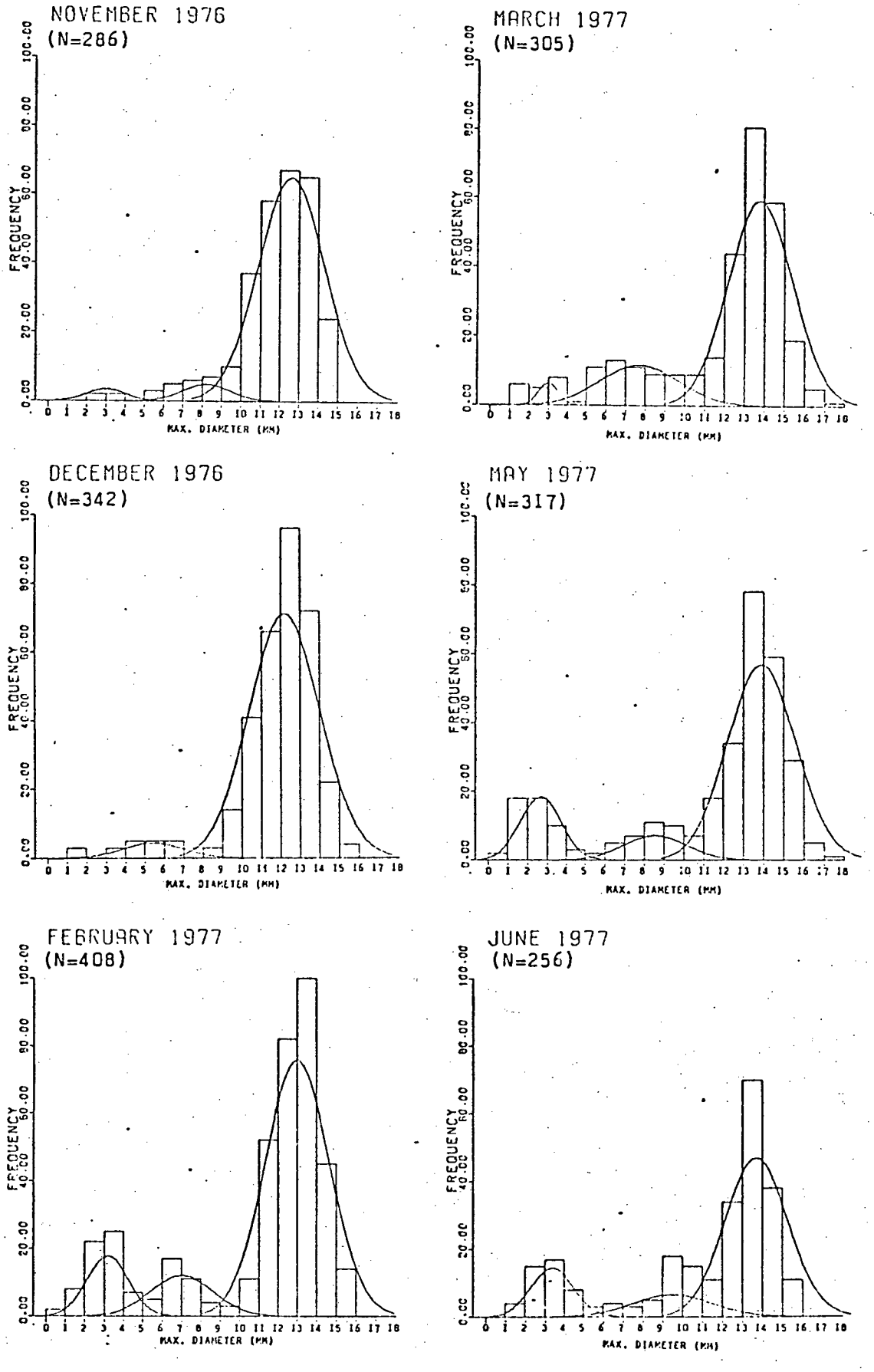

NOVEMBER 1976
(N=286)
MARCH 1977
(N=305)
DECEMBER 1976
(N=342)
MAY 1977
(N=317)
FEBRUARY 1977
(N=408)
JUNE 1977
(N=256)
FREQUENCY
MAX. DIAMETER (MM)

Fig. 2.32

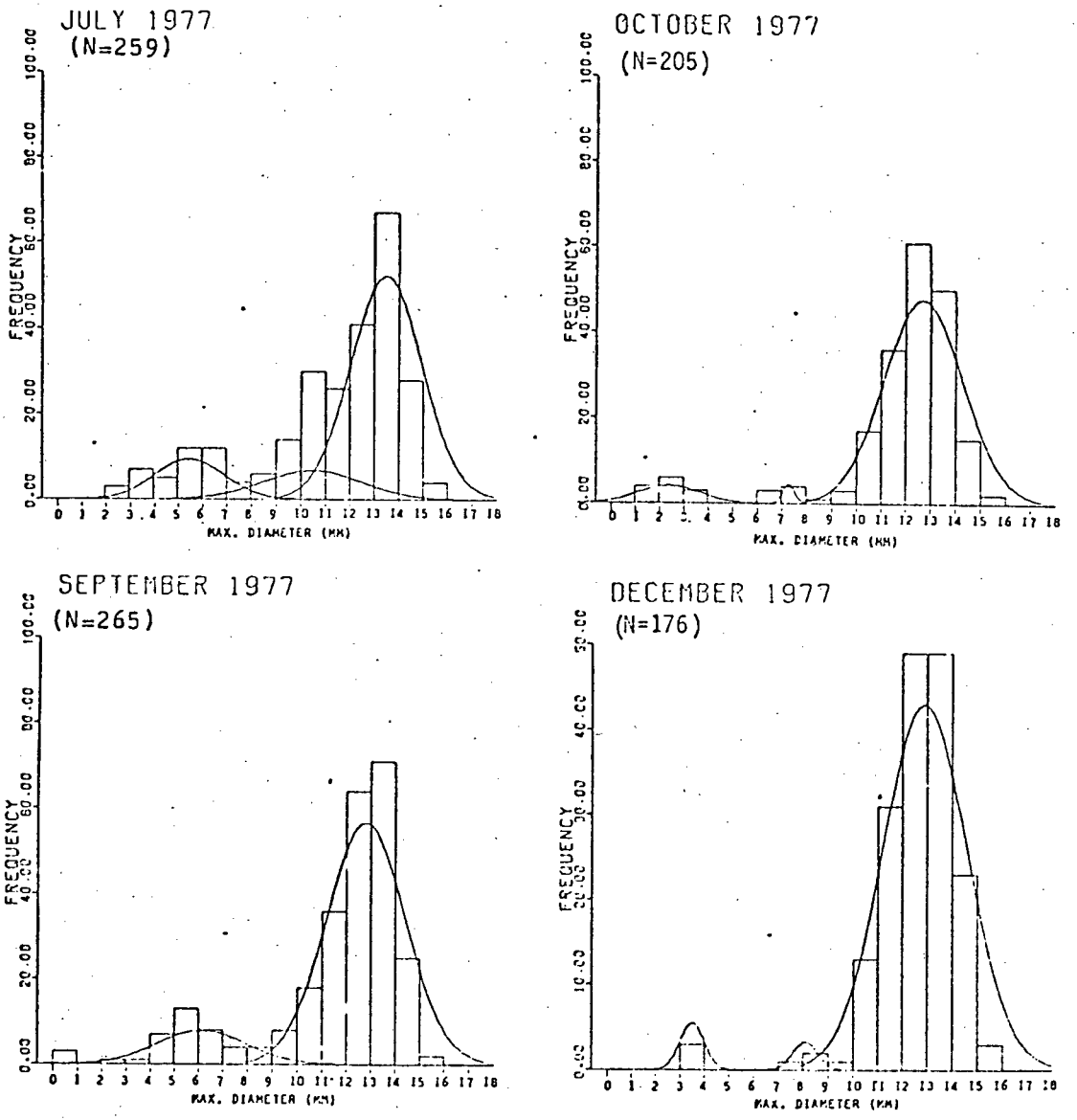


Fig. 2.32 (Cont'd)

Fig. 2.33 : Size frequency distribution for Oxystele variegata in zone 3 at Dalebrook at six-weekly intervals from November 1976 to December 1977. Normal distribution curves plotted for each cohort as in fig. 2.30.
N indicates sample size.

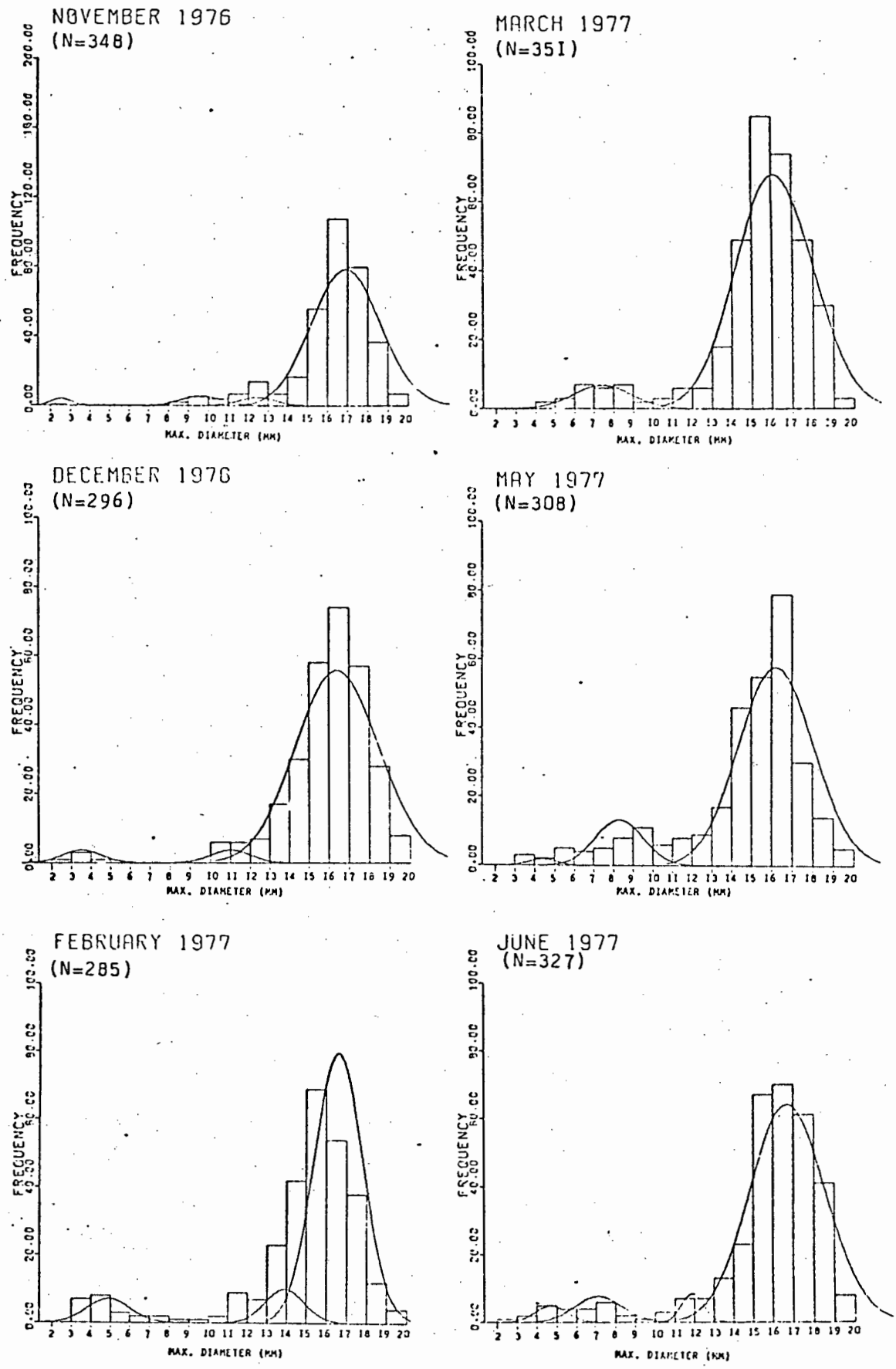

NOVEMBER 1976
(N=348)
FREQUENCY
MAX. DIAMETER (MM)
MARCH 1977
(N=351)
FREQUENCY
MAX. DIAMETER (MM)
DECEMBER 1976
(N=296)
FREQUENCY
MAX. DIAMETER (MM)
MAY 1977
(N=308)
FREQUENCY
MAX. DIAMETER (MM)
FEBRUARY 1977
(N=285)
FREQUENCY
MAX. DIAMETER (MM)
JUNE 1977
(N=327)
FREQUENCY
MAX. DIAMETER (MM)

Fig. 2. 33

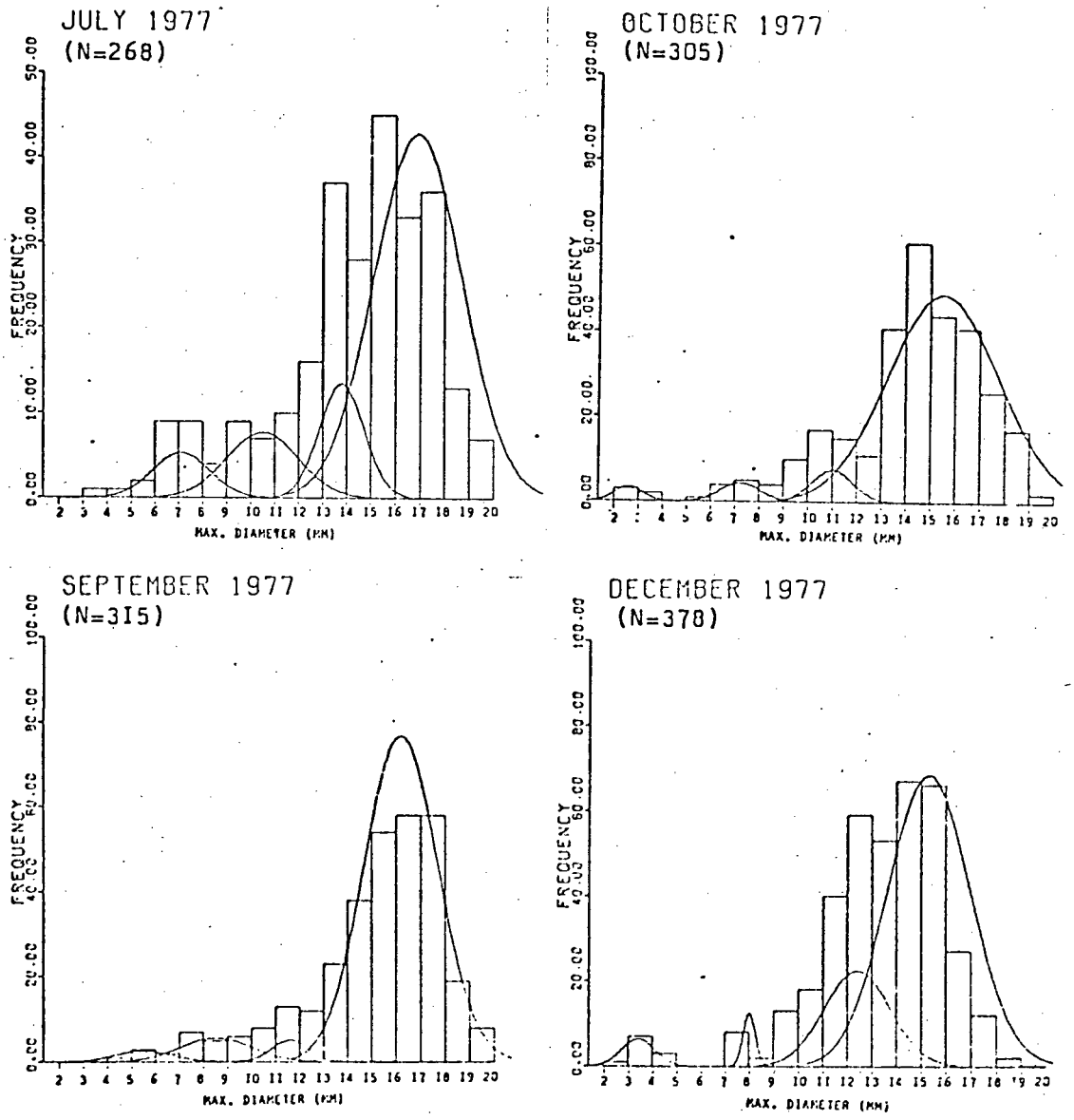


Fig. 2.33 (Cont'd)

Zone 3 (fig. 2.33) was clearly dominated by the 16-18 mm size class even when settlement in the lower zones was high. Settlement in zone 3 was very limited so that few juveniles appeared. Summer (December/February), winter (June/July) and spring (October) settlements are discernible but less obvious as very small numbers of juveniles are involved.

Settlement thus decreased markedly up the shore, the main settlement period occurring in February 1977 with a much smaller recruitment in May 1977 and a few juveniles appearing in October 1977 (fig. 2.30). The predominance of progressively larger animals going up the shore is attributable to upshore migration between the zones on size dependent basis. Zone 3 is the highest zone and was dominated by precisely the size classes absent from zones 2 and 3 (ie. 16-18 mm). Animals of up to 22 mm also occurred in zone 3 but were absent from the lower zones. Recruitment is thus due to larval settlement in zone 1, and in zone 2 to a lower level of settlement and migration from zone 1. Recruitment in zone 3 is due almost entirely to immigration from the lower zones.

2. Maintenance of size gradients

(a) Migration

Transplanting experiments revealed that juveniles or adults moved to zones of the shore where they do not normally occur rapidly return up or downshore to their original zones. Data on the direction of dispersal of marked animals for 1, 5 and 9 days after release are given in figs. 2.34 and 2.35. Adult animals placed in the lower balanoid (zone 1) show a very clear movement upshore (fig. 2.34) while juveniles placed in the upper balanoid (zone 3) show the reverse (fig. 2.35). In both cases χ^2 tests indicate non-random dispersal of experimental animals ($P < 0{,}001$) and random dispersal of controls ($P > 0{,}05$). The rate of dispersal, expressed as mean distance of recovered animals from the point of release, is given for experimental and control animals in figs. 2.36 and 2.37. Dispersal was much quicker for the larger, more mobile adults, the first of which had returned to its home zone (a distance of approximately 27m) within 3 days. After 9 days most of the recovered adults had returned to zone 3 so that mean distance levelled

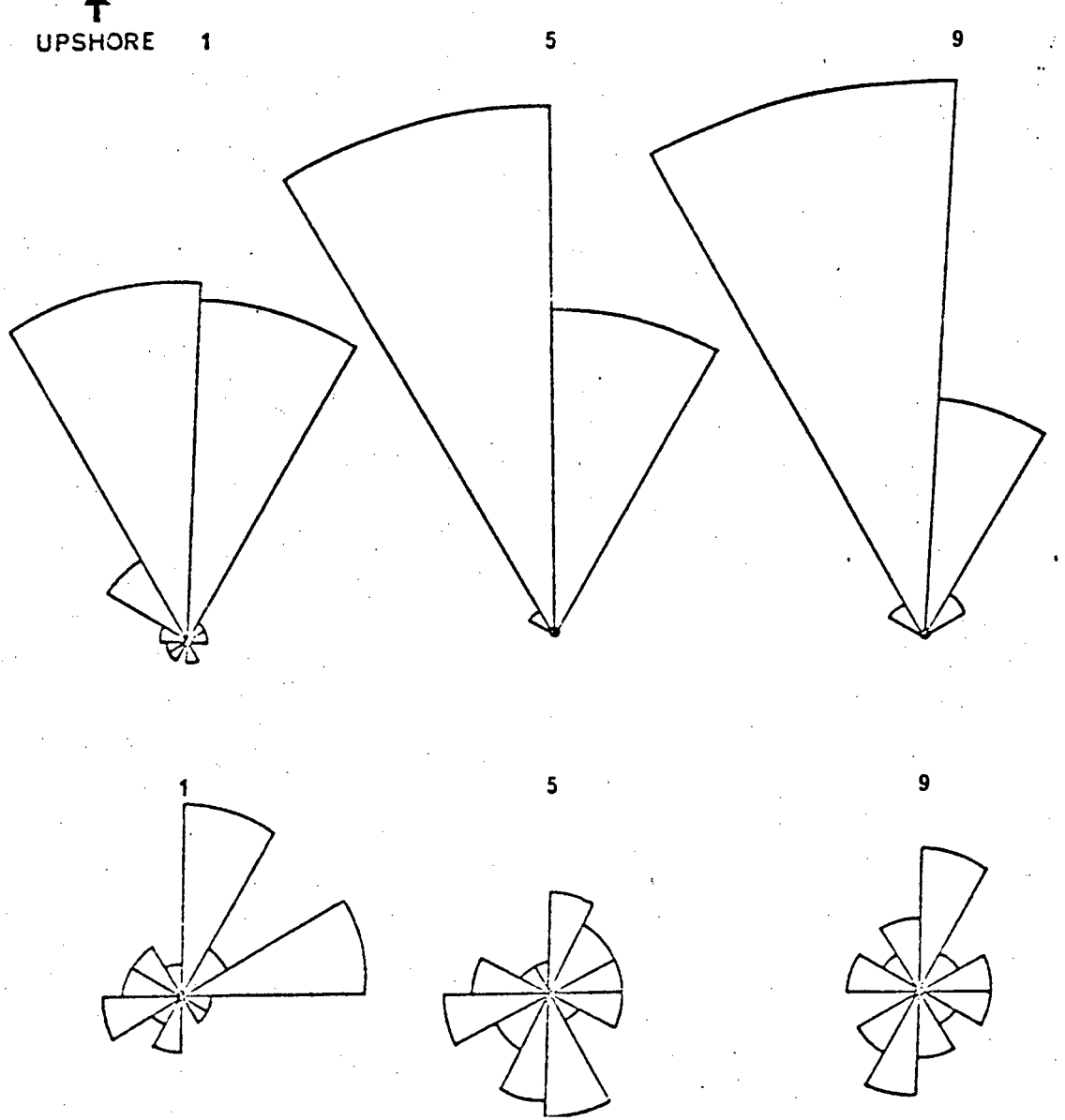


Fig. 2.34 : The direction of dispersal of marked adult O. variegata 1, 5 and 9 days after release. Experimental animals upper figures, control animals lower. (——— = 10 % of sample)

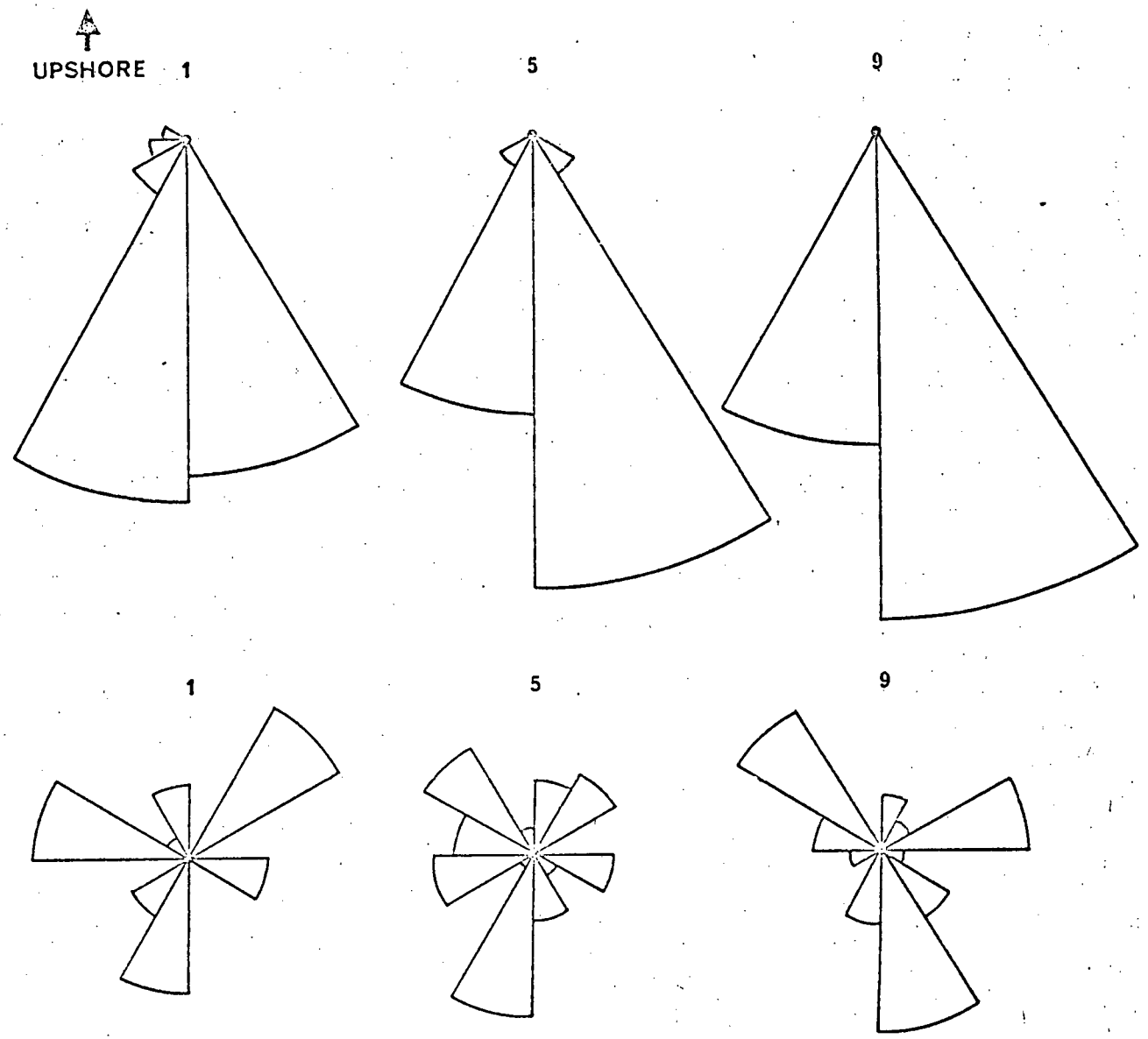


Fig. 2.35 : The direction of dispersal of marked juvenile O. variegata 1, 5 and 9 days after release. Experimental animals upper figures, control animals lower. (——— = 10 % of sample)

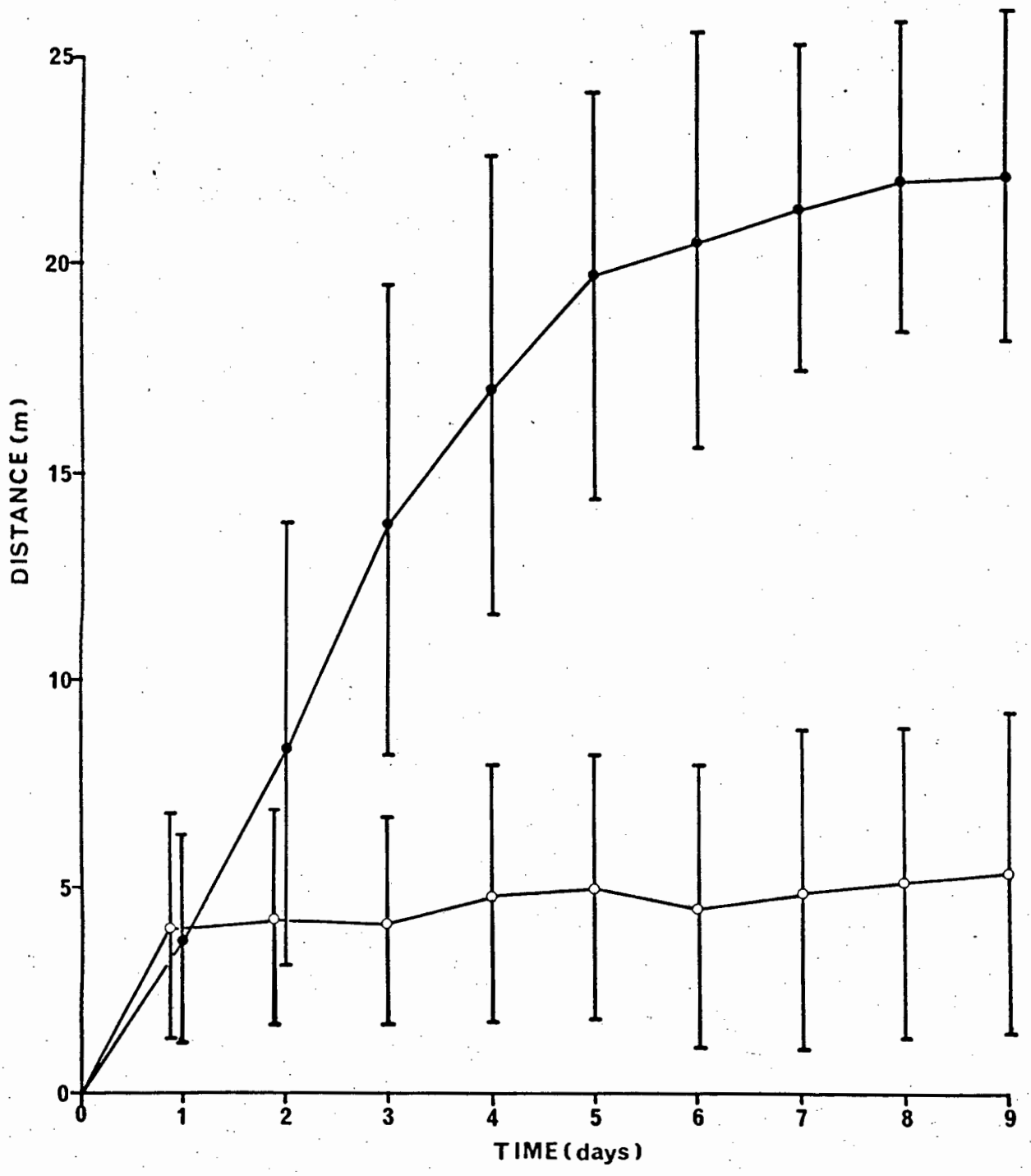


Fig. 2.36 : The mean distance (± S.D.) of marked samples of adult O. variegata from the release point with time.

● = experimental o = control

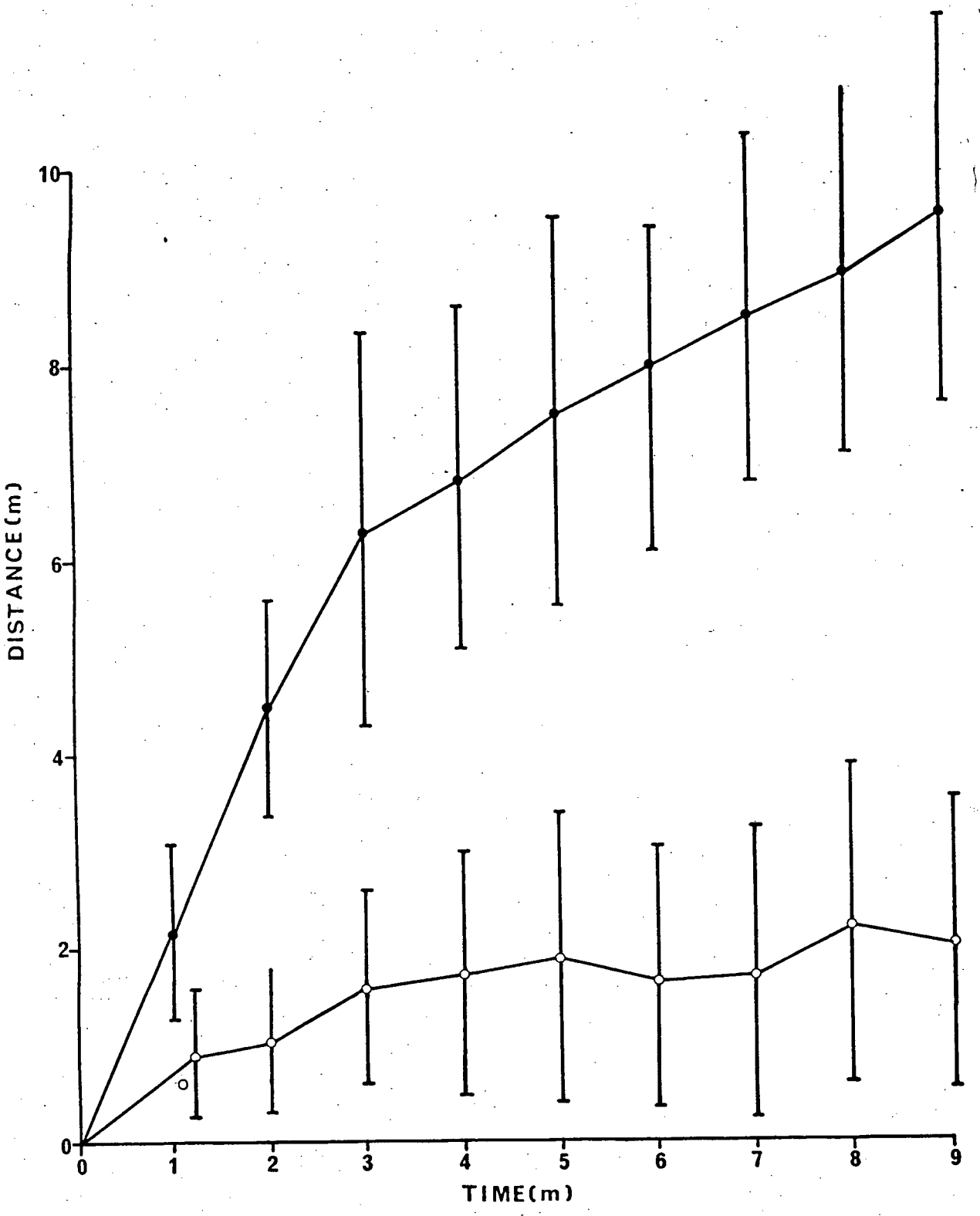


Fig. 2.37 : The mean distance (± S.D.) of marked samples of juvenile O. variegata from the release point with time.

● = experimental o = control.

off after day 5. Very few juveniles had reached zone 1 after 9 days so that mean distance for the sample continued to increase. In both cases control animals dispersed much more slowly and mean distance quickly levelled off, reflecting random dispersal.

(b) Caging experiments

Caging of adult and juvenile animals in the reversed zones resulted in rapidly reduced ecological performance when compared with control animals caged in their normal zones. Shell diameter/dry body weight regression curves for lower and upper balanoid samples of adult animals are given in figs. 2.38 and 2.39. There was no mortality in either sample and t-tests indicate no significant difference in the slope of the two regression curves ($P > 0,05$). The intercept however was significantly higher for the lower balanoid sample ($P < 0,01$).

Mortality of caged juvenile animals is given for both zones in fig. 2.40. There was no mortality in the lower balanoid cages while 38 of the original 40 animals in the upper balanoid were dead within 5 days.

Table 2.8 reveals that primary productivity decreases rapidly in an upshore direction. It should also be noted that the values obtained are all much higher than those obtained for the Littorina zone over the same period (c.f. Table 2.4).

TABLE 2.8: CHLOROPHYLL a CONCENTRATION ON PRODUCTIVITY STRIPS EXPOSED IN THE BALANOID ZONE FOR 90 DAYS (GIVEN AS MEANS FOR 10 VALUES ± S.D.)

	ZONE		
	Upper	Middle	Lower
Chl. a concentration ($\mu g.cm^{-2}$)	76,1 ± 9,8	117,7 ± 4,8	159,4 ± 10,6

(c) Resistance to desiccation

(i) The relationship between body volume and opercular diameter is expressed as a power curve in fig. 2.41. This relationship indicates a relatively larger opercular surface area for potential water loss in smaller animals.

(ii) The relationship of body size to rate of water loss is represented by a steep power curve (fig. 2.42). Rates of water loss over a 4 hour period are very high for small animals, actually exceeding lethal limits. In addition to high rates of water loss small animals

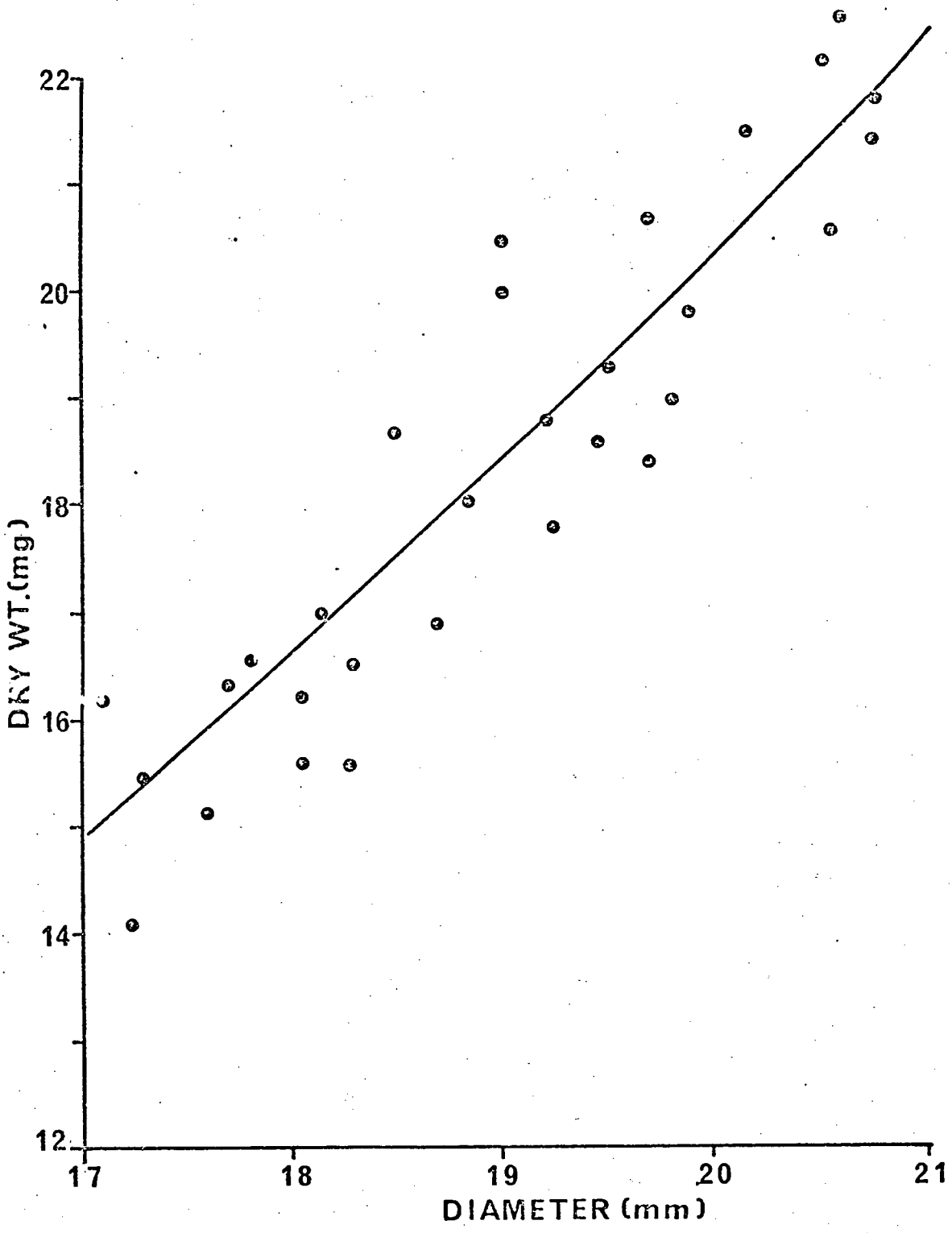


Fig. 2.38 : The relationship between maximum shell diameter and shell-free dry body weight for adult O. variegata caged in the lower balanoid (zone 1).

$y = 0{,}0616\ x^{1{,}9372}$ $(r = 0{,}91)$

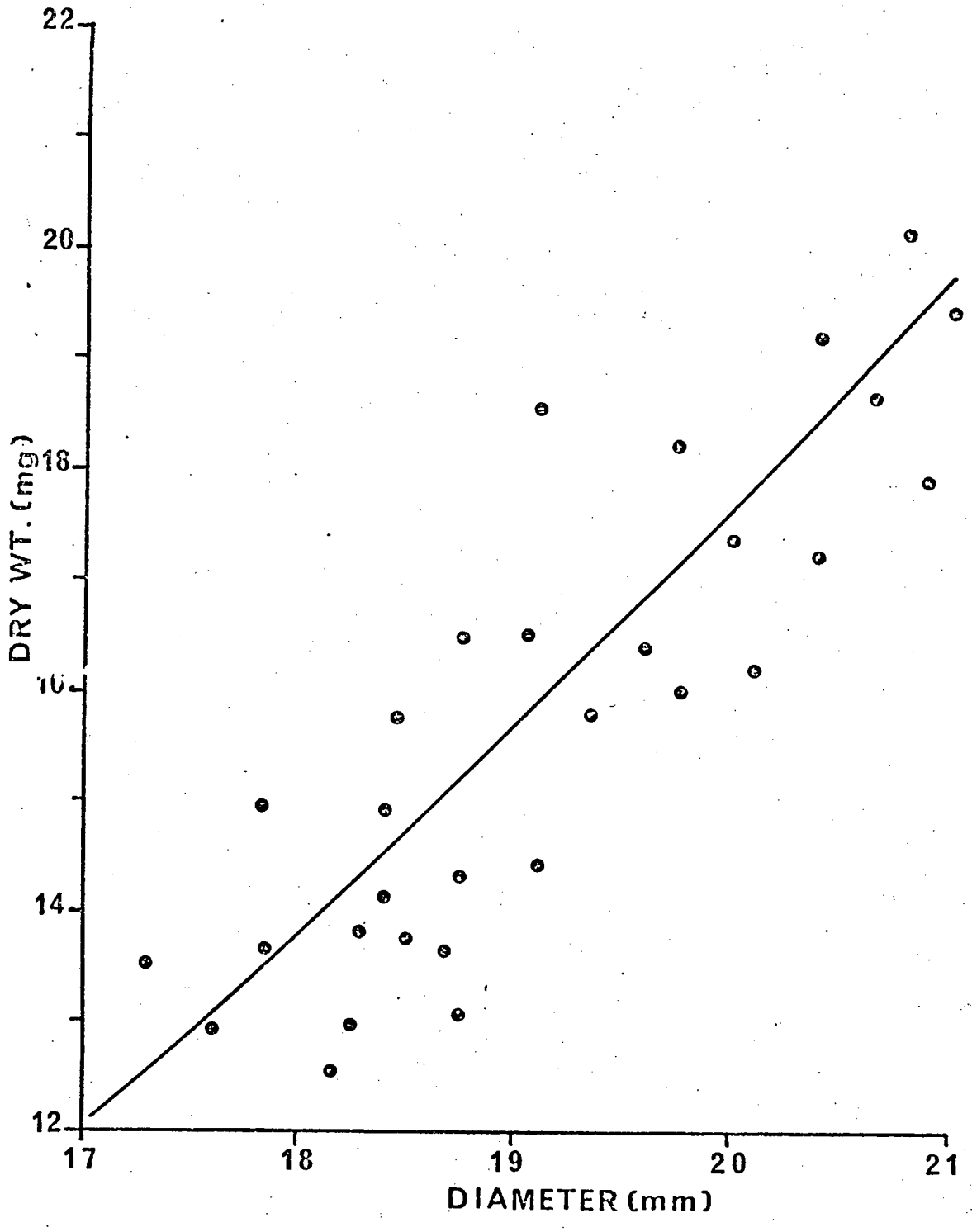


Fig. 2.39 : The relationship between maximum shell diameter and shell-free dry body weight for adult O. variegata caged in the upper balanoid (zone 3).

$y = 0{,}0157\ x^{2{,}3432}$ $(r = 0{,}83)$

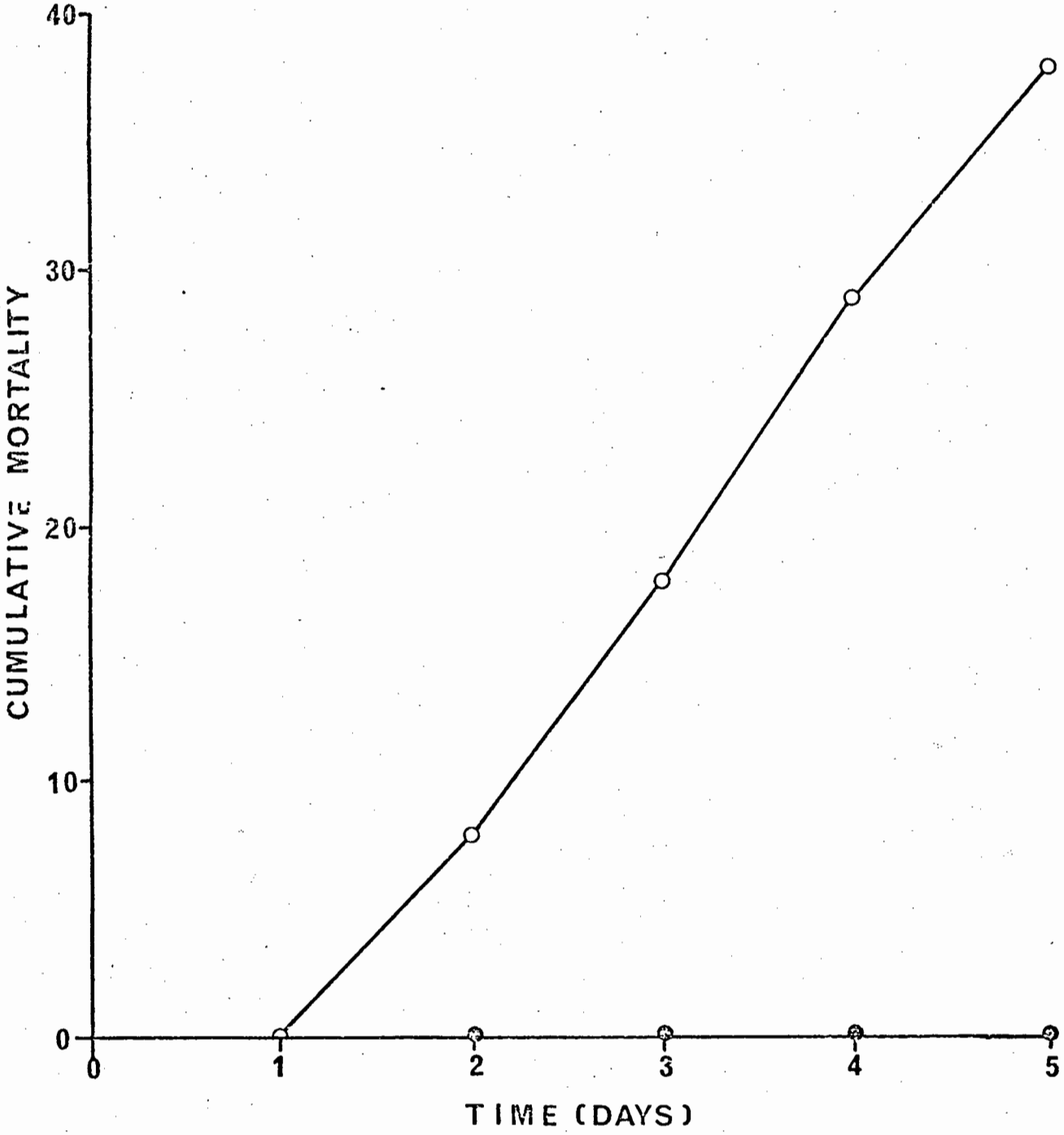


Fig. 2.40 : Cumulative mortality of juvenile O. variegata caged in the lower (zone 1) and upper balanoid (zone 3).

● = lower balanoid O = upper balanoid

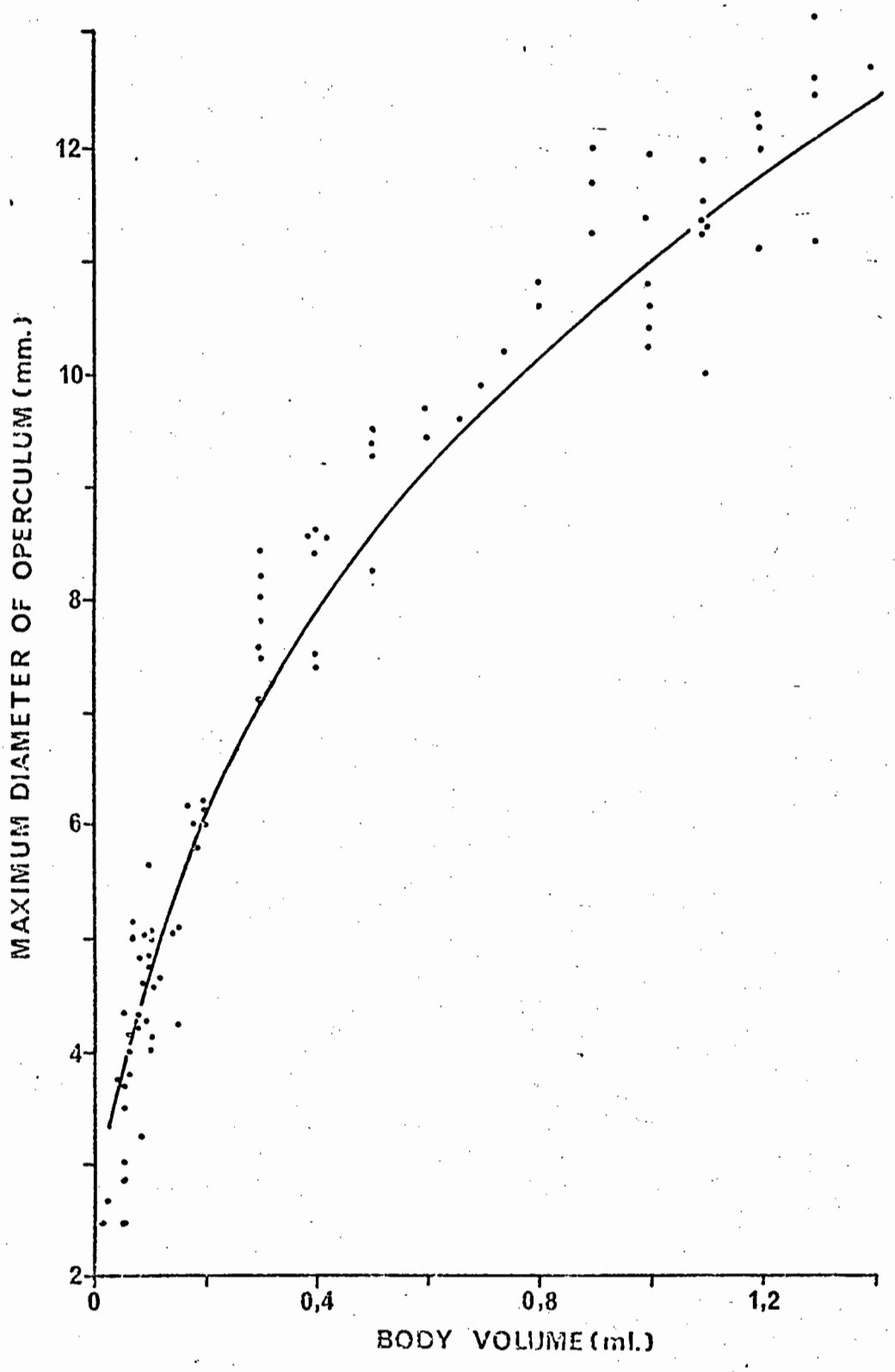


Fig. 2.41 : The relationship between body volume of O. variegata and maximum opercular diameter

$$y = 11{,}05 \times^{0{,}37} \quad (r = 0{,}95)$$

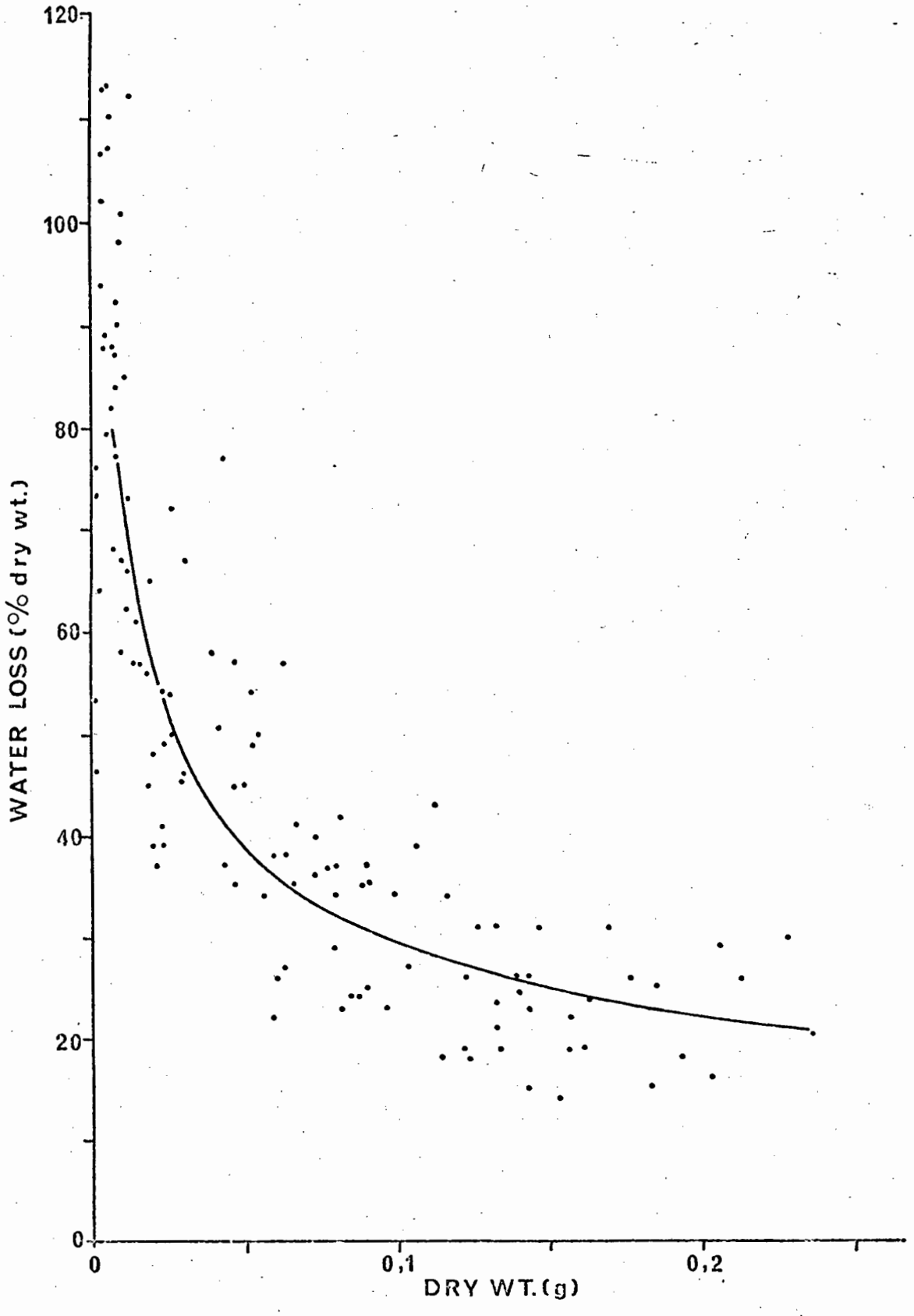


Fig. 2.42 : The relationship between shell-free dry body weight of O. variegata and water loss over a period of 4 hr. Water loss is expressed as % dry weight.

$$y = 12{,}07 \times^{-0{,}3910} \quad (r = 0{,}84)$$

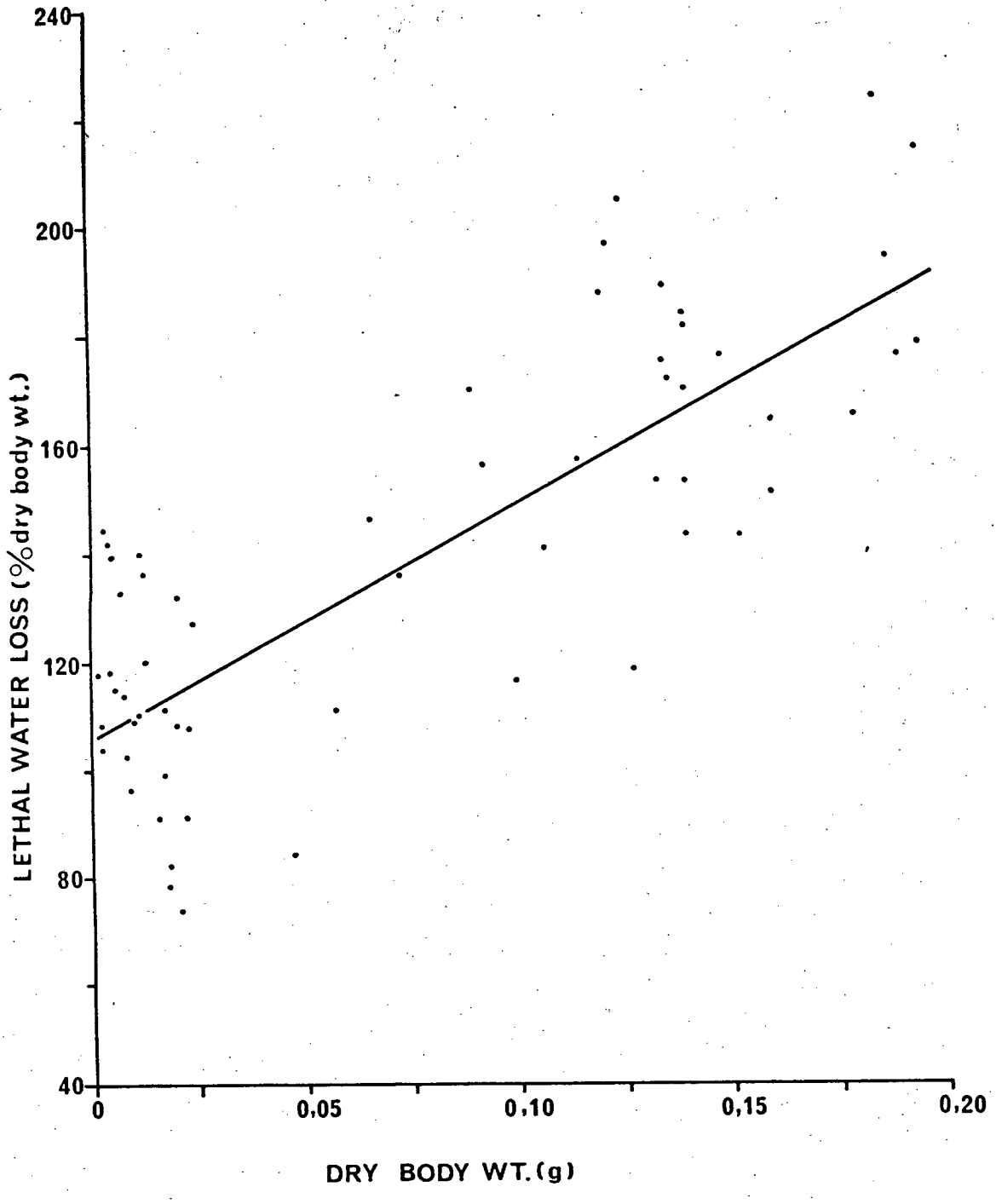


Fig. 2.43 : The relationship between shell-free dry body weight of O. variegata and lethal water loss (expressed as % dry weight)
$y = 105{,}29 + 434{,}59\,x$ $(r = 0{,}69)$

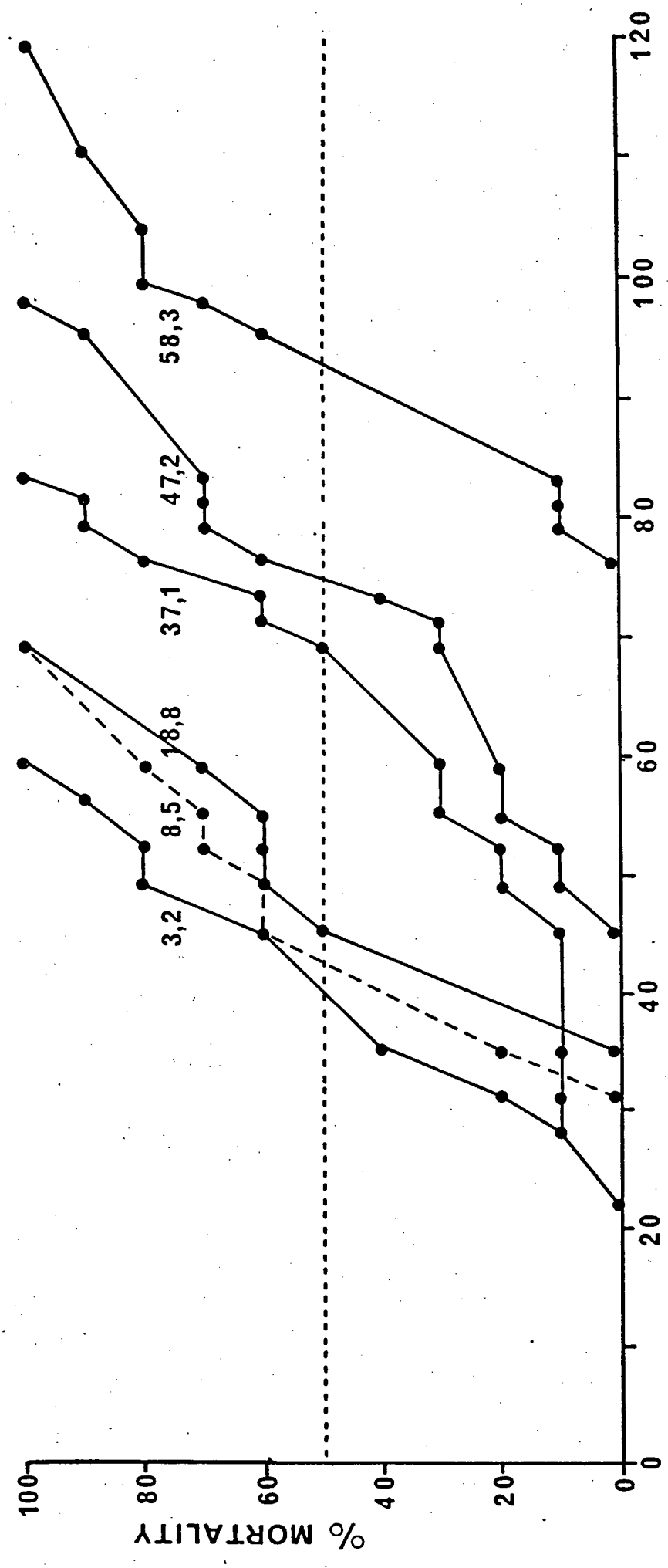


Fig. 2.44 : Cumulative mortality of adult O. variegata exposed to low humidities. Figures on each line indicate % relative humidity.

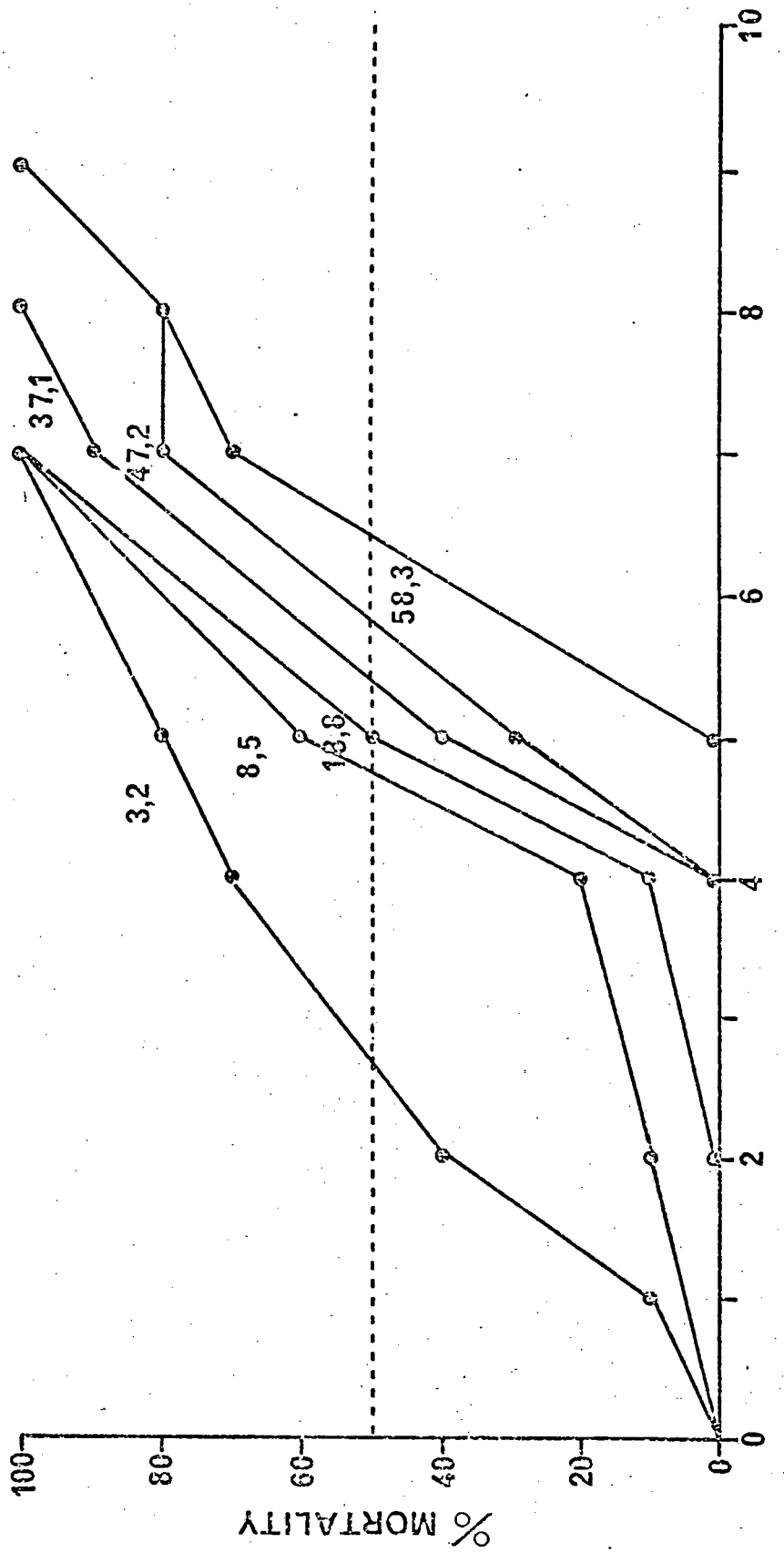


Fig. 2.45 : Cumulative mortality of juvenile O. variegata exposed to low humidities. Figures on each line indicate % relative humidity.

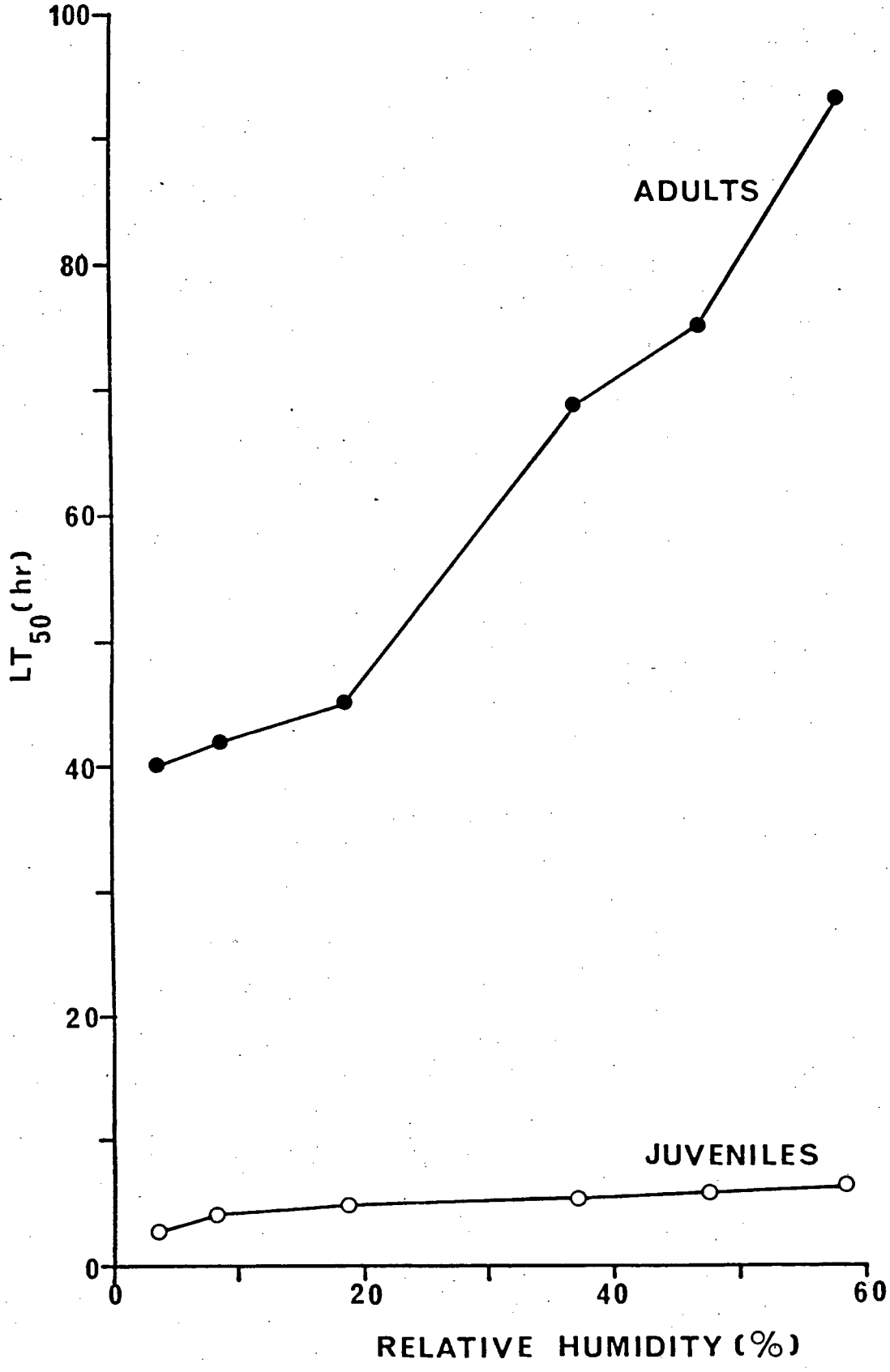


Fig. 2.46 : The relationship between humidity and the time required for 50 % mortality (LT_{50}) of samples of O. variegata.

also exhibit a much lower resistance to desiccation than adults. A linear relationship exists between dry body weight and lethal percentage water loss (fig. 2.43).

(iii) Data on cumulative mortality at low humidities (figs. 2.44 and 2.45) were used to derive LT_{50} values (ie. the time required for mortality of 50 % of the samples) for adults and juveniles over a range of humidities (fig. 2.46). High rates of water loss combined with a low resistance to desiccation lead to a much faster death rate for juveniles than for adults at any particular humidity. LT_{50} for juveniles increases only slightly as humidity rises, presumably due to their extreme sensitivity to water loss (fig. 2.43).

(d) Predation

Figs. 2.47 and 2.48 show predation rates on adults in zones 1 and 3 (lower and upper balanoid respectively) during two separate experiments. Although these rates are artificially high (as tethering impairs escape behaviour) predation is obviously much greater on the lower shore. The whelk Burnupena delalandii was observed attacking tethered and untethered O. variegata on some 6 or 7 occasions and high predation rates in the lower balanoid are attributable to its much greater abundance in that zone.

3. Population dynamics

(a) Total population size

The total population reached a maximum in February 1977 due to heavy settlement and then declined for the remainder of the sampling period, with a slight increase in May 1977 when recruitment again rose (fig. 2.49). Mortality of juveniles settling in February 1977 (cohort B on fig. 2.30) was very high (see below). When these animals merged with the older cohort A in September 1977 the combined cohort remained much smaller than cohort A had been in November 1976 (fig. 2.50). Settlement after February 1977 was limited and recruitment was insufficient to balance mortality. Consequently total population declined and in December 1977 it was 30,80 % lower than a year earlier in December 1976 (fig. 2.49).

(b) Mortality

Mortality may be estimated from these data on the assumption that migration occurs up the shore only and not horizontally into or out of the overall population. This assumption is based on the fact that a very large area of beach was considered which is physically isolated from neighbouring areas by deep gulleys.

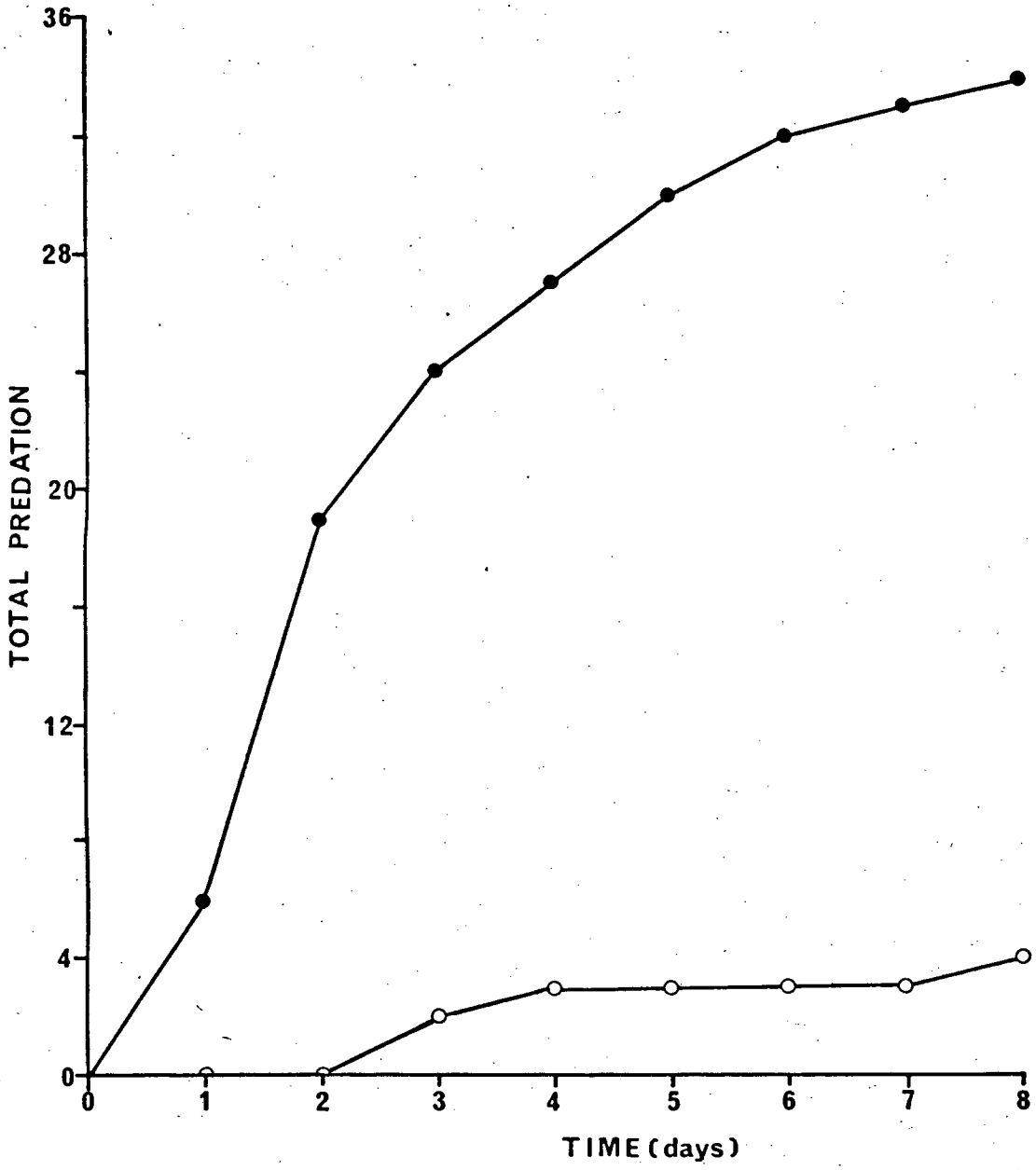


Fig. 2.47 : Cumulative predation of tethered samples of O. variegata
● = lower balanoid (zone 1) o = upper balanoid (zone 3)
Experiment 1.

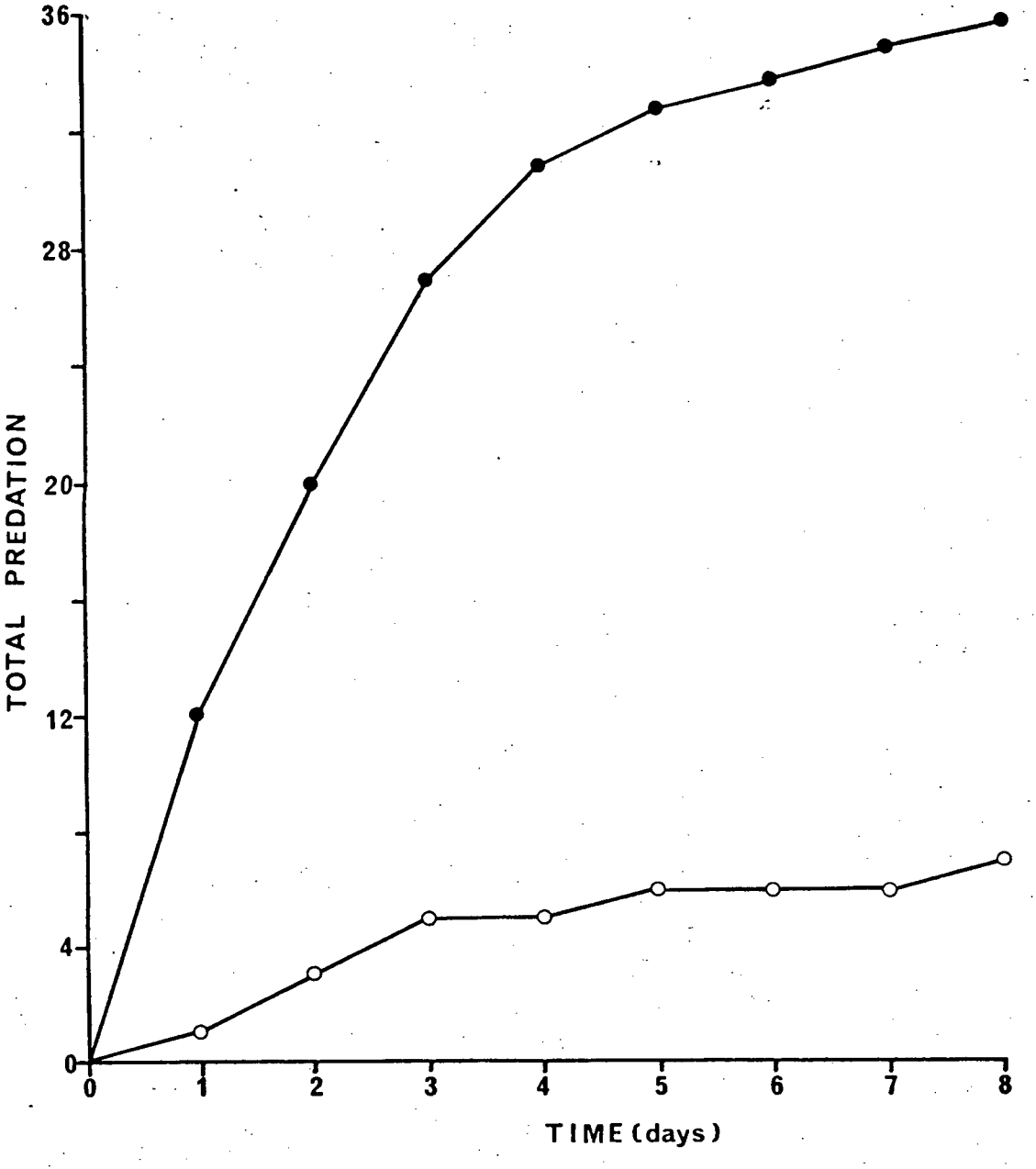


Fig. 2.48 : Cumulative predation of tethered samples of O. variegata
● = lower balanoid (zone 1) o = upper balanoid (zone 3)
Experiment 2.

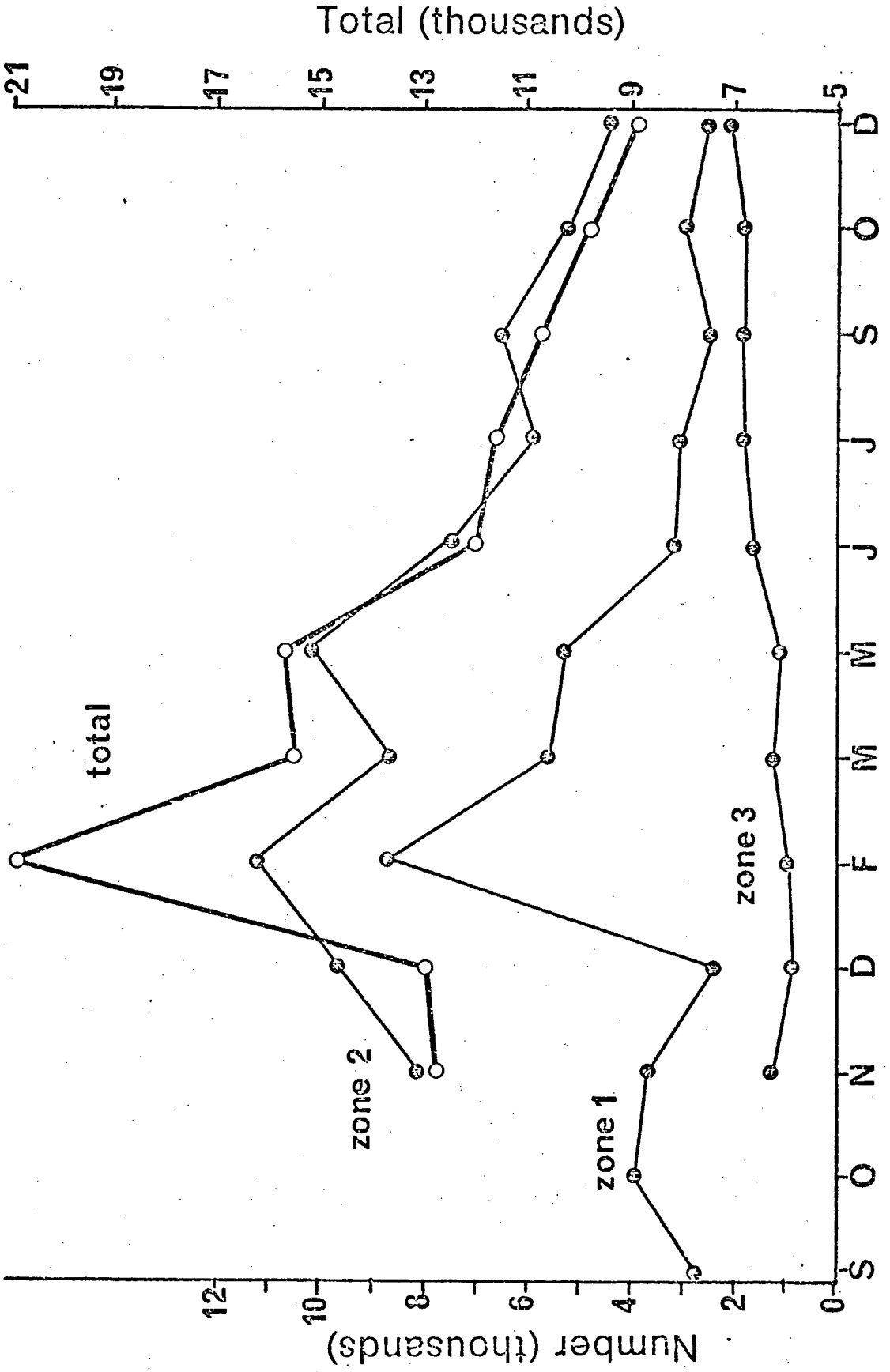


Fig. 2.49 Numbers of Oxystele variegata in each zone examined and total population size from November 1976 to December 1977 (derived at six-week intervals).

Migration between zones means that mortality can be estimated for the population as a whole but not for each zone separately. To derive mortality rates size frequency data for the entire population (fig. 2.30) were subjected to cohort analysis as described for growth rates. The programme NORMSEP derives the percentage of total population in each cohort so that the absolute size of each cohort may be derived. Cohort size is plotted against time in fig. 2.50 for the four cohorts recognized. Cohort D was sampled only twice, at the end of the sampling period, and data for cohort C show irregular fluctuations due to extended recruitment into this cohort. Data for cohorts A and B however may be used to derive mortality rates for adult and juvenile animals respectively. These two cohorts slowly converged due to the effects of age dependent growth rates. However they are separable using NORMSEP, even in the region of overlap, up to the point where they combined to form a single, normally distributed cohort in September 1977 (fig. 2.50). Because of this each cohort may be treated as a separate unit, experiencing no recruitment and slowly declining in size due to mortality until they combine in September 1977 to form a large merged cohort. For cohort B recruitment ended after February 1977 as a new juvenile cohort (cohort C) appeared in March 1977 (fig. 2.30).

Overlap of cohorts A and B became particularly great in July 1977 and mortality of adult animals (cohort A) may be derived for November 1976 - June 1977 as a decline of 3998 animals. This was a drop of 32,64 % from the November value, in 8 months, yielding a monthly mortality of 4,08 % or 48,96 % .year^{-1}. Mortality for a newly settled cohort (cohort B) was much higher with a decline of 4741 animals in 5 months from February-June 1977. This is 62,18 % of the February value ie. 12,44 % .month^{-1}. Thus mortality of small juveniles is very high but declines markedly for animals which survive to 13-14 mm.

Mortality rates for these two cohorts may be expressed as regressions of numbers against time. Numbers .m^{-2} were plotted on a logarithmic scale following Shafir (1978) with time as six-week sampling intervals in fig. 2.54. The equations derived were :

Cohort A $\log_{10} N = 4,07 - 0,03t \quad (r = 0,92)$

Cohort B $\log_{10} N = 4,12 - 0,16t \quad (r = 0,93)$

Fig. 2.50 : Total numbers of Oxystele variegata in cohorts A-D and the combined cohort A + B identified from data on total population size distribution. Samples were collected at six-week intervals from November 1976 to December 1977.

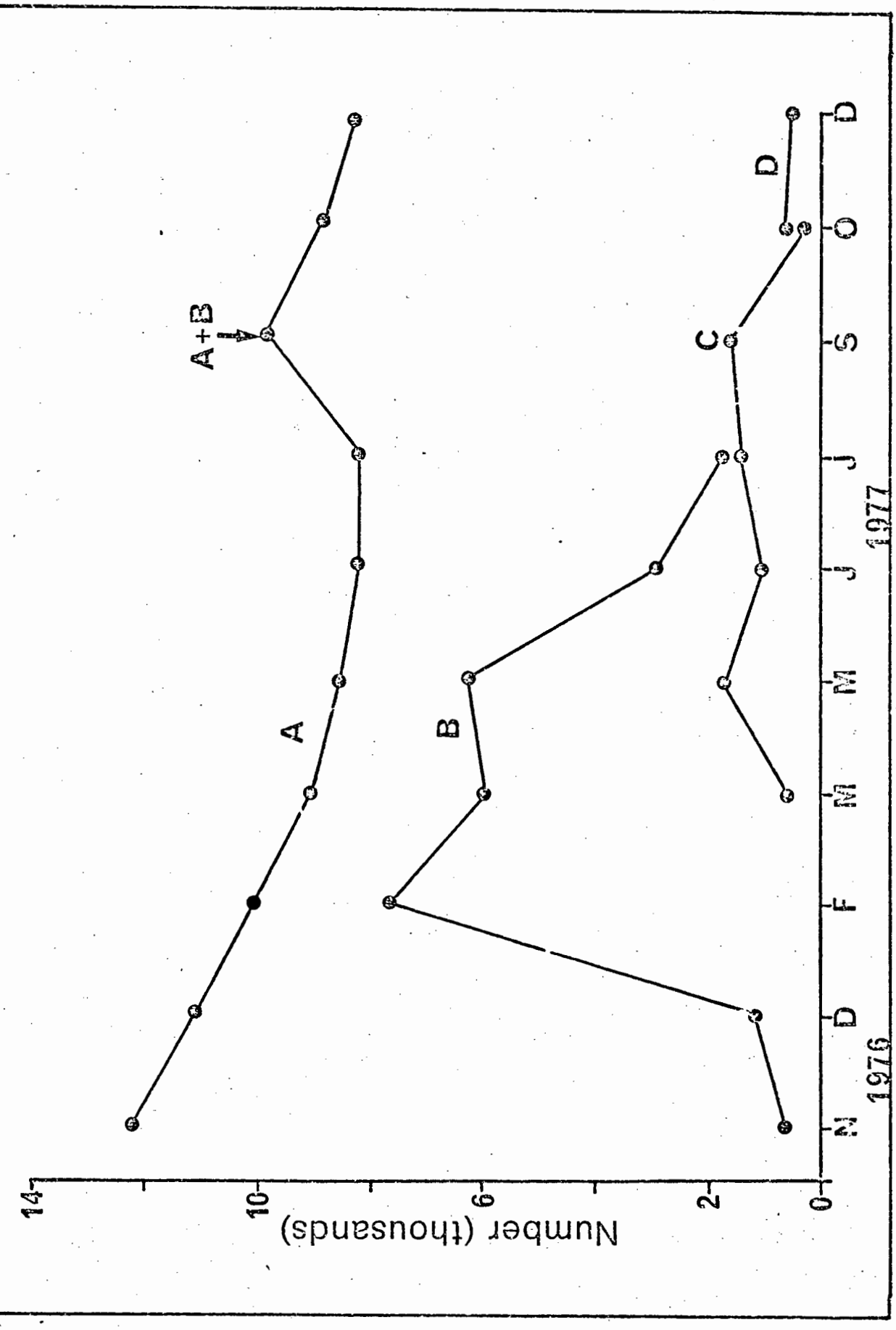


Fig. 2.50

(c) Numerical distribution

The percentage of total population present in each zone is given in Table 2.9.

TABLE 2.9 : PERCENTAGE OF TOTAL POPULATION IN ZONES 1-3

MONTH	ZONE 1	ZONE 2	ZONE 3
1976			
November	27,89	62,15	9,96
December	18,22	74,74	7,04
1977			
February	41,20	54,10	4,60
March	37,20	55,13	7,67
May	40,91	53,75	5,34
June	26,23	59,96	13,81
July	26,59	51,73	21,68
September	25,35	59,50	15,15
October	29,52	52,20	18,28
December	29,01	47,96	23,03

Zone 2 contained the highest numbers as well as highest density (c.f. Table 2.10)generally forming 50-60 % of total population. Numbers increased in zones 1 and 2 during settlement in February 1977. Settlement was particularly heavy in zone 1 and the contribution of this zone to total population rose accordingly (Table 2.9). The limited nature of settlement in zone 1 after February was reflected in a steady decline in numbers with a slight increase in October 1977 (c.f. fig. 2.49). Likewise numbers in zone 2 increased in May 1977 due to settlement and then continued to decline.

The pattern of numerical distribution in each zone shown in fig. 2.49 provides further evidence of migration between zones. Numbers in zone 1 decreased from November to December 1977 despite a small settlement in December. This was synchronous with an increase in population in zone 2. Likewise between July and September 1977 population at zone 2 increased by a number similar to the decrease in zone 1.

Although total population and population in zones 1 and 2 decreased after February 1977 numbers in zone 3 gradually increased over the same period. This was particularly obvious after May when numbers in zones 1 and 2 decreased most rapidly. The increase in zone 3 did not entirely account for the decline in the lower two zones, which was partly due to mortality, and there was a drop in total population.

(d) Density

Mean densities $.m^{-2}$ for each zone throughout the sampling period are given in Table 2.10. Distribution in zone 3 is however extremely clumped so that density may be locally much greater. Therefore in dealing with population size the total population for each zone and for the entire area occupied (approximately 420 m^2) were considered. These data follow the same pattern as density changes during the year.

TABLE 2.10: MEAN DENSITY $.m^{-2}$

MONTH	ZONE 1	ZONE 2	ZONE 3
1976			
November	26,00	54,00	9,66
December	17,00	65,00	6,83
1977			
February	62,25	76,00	7,20
March	42,00	57,99	9,00
May	49,00	60,00	6,65
June	23,00	49,00	12,59
July	22,00	39,89	13,72
September	19,76	43,21	13,78
October	21,03	34,66	13,55
December	18,06	29,14	15,61

(e) Biomass

Mean biomass was calculated as acidised dry mass $.m^{-2}$ from size frequencies densities and the length/weight equation and is plotted for each zone in fig. 2.51. Biomass was highest in zone 2 due to a much

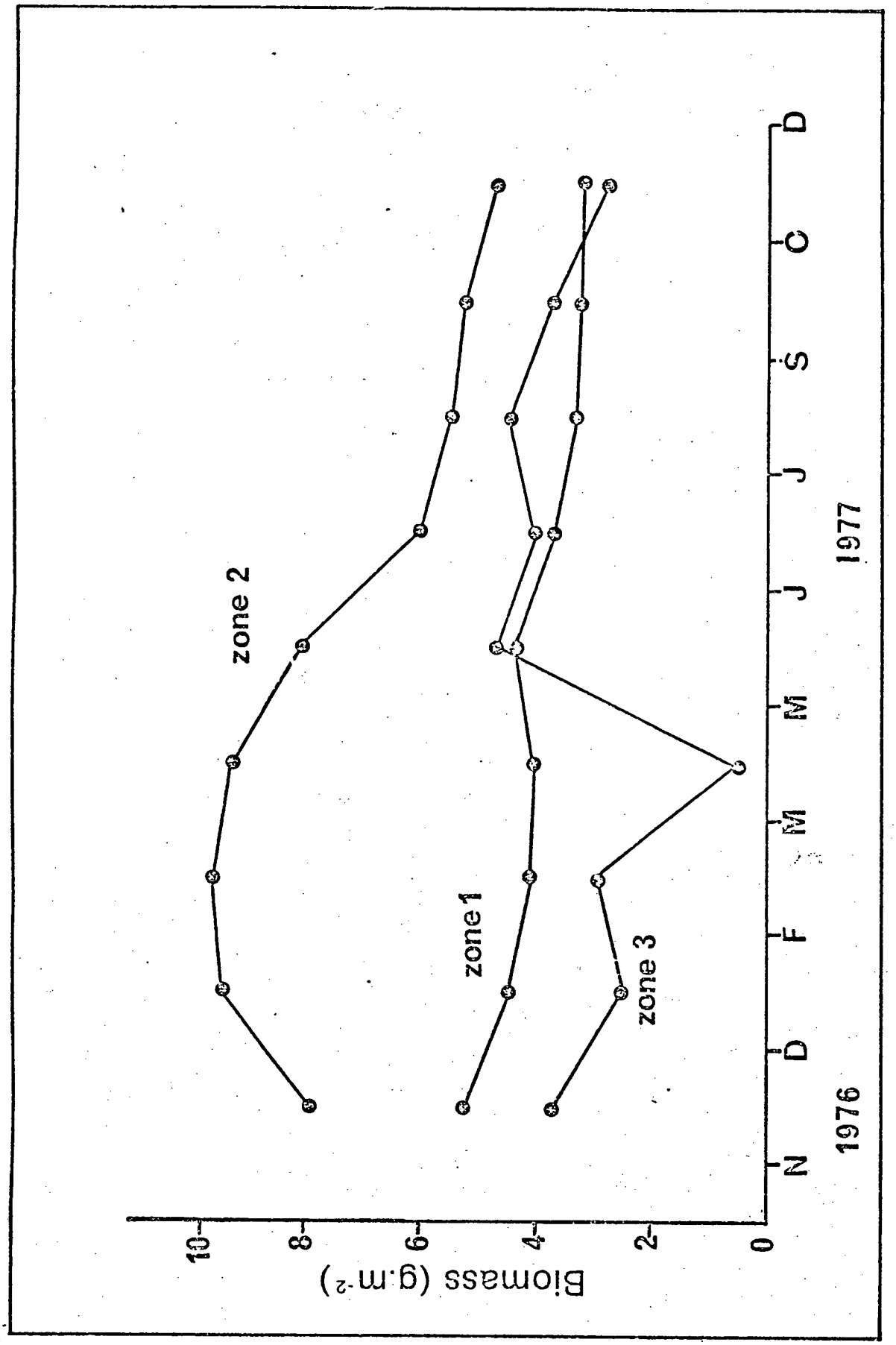


Fig. 2.51 Biomass (acidised dry mass $.m^{-2}$) of Oxystele variegata in zones 1-3 at six-weekly intervals from November 1976 to December 1977. Points are plotted as 12-weekly running means.

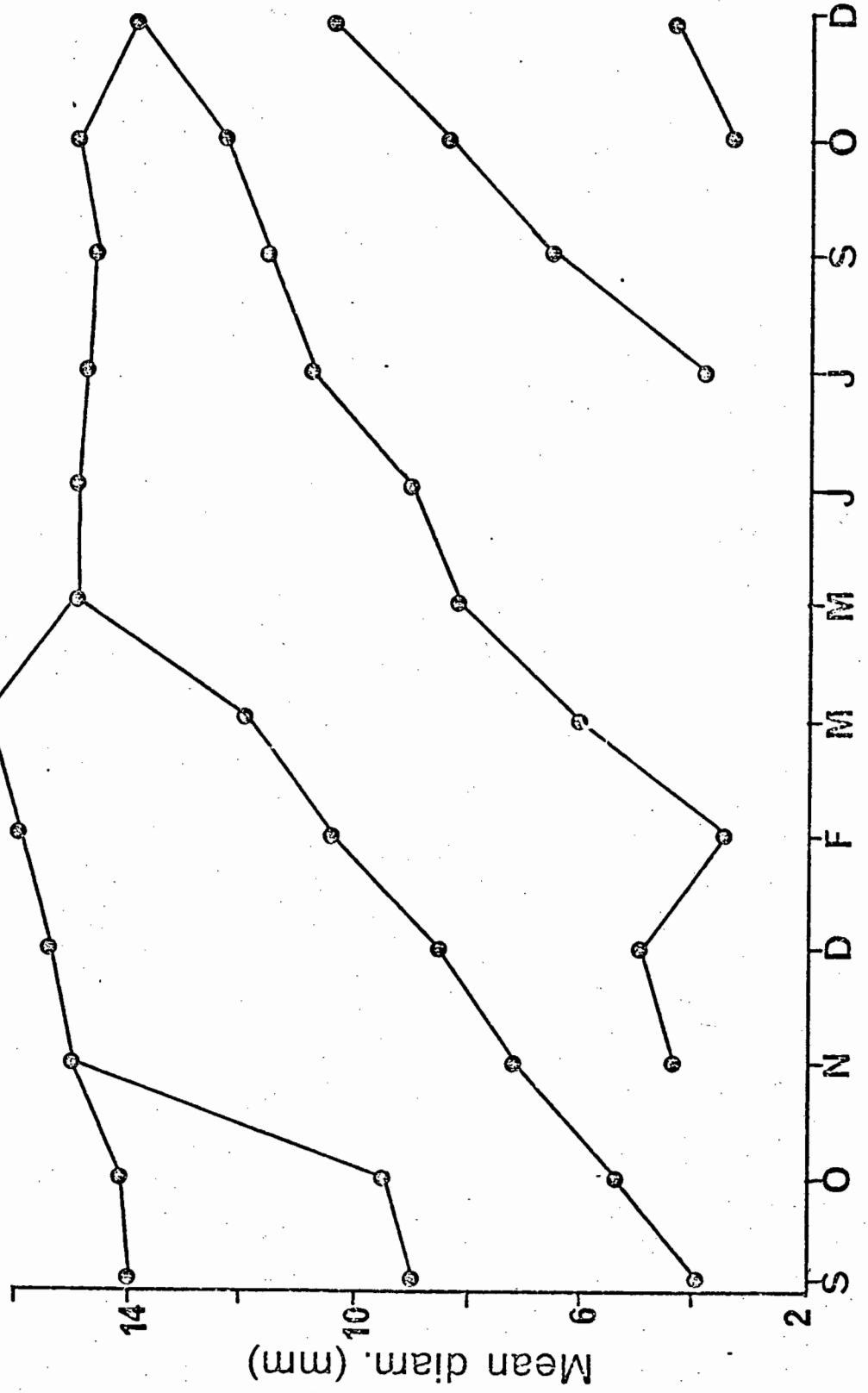


Fig. 2.52 Composite growth curves for Oxystele variegata in zones 1-3 derived from figs. 2.30-2.33.

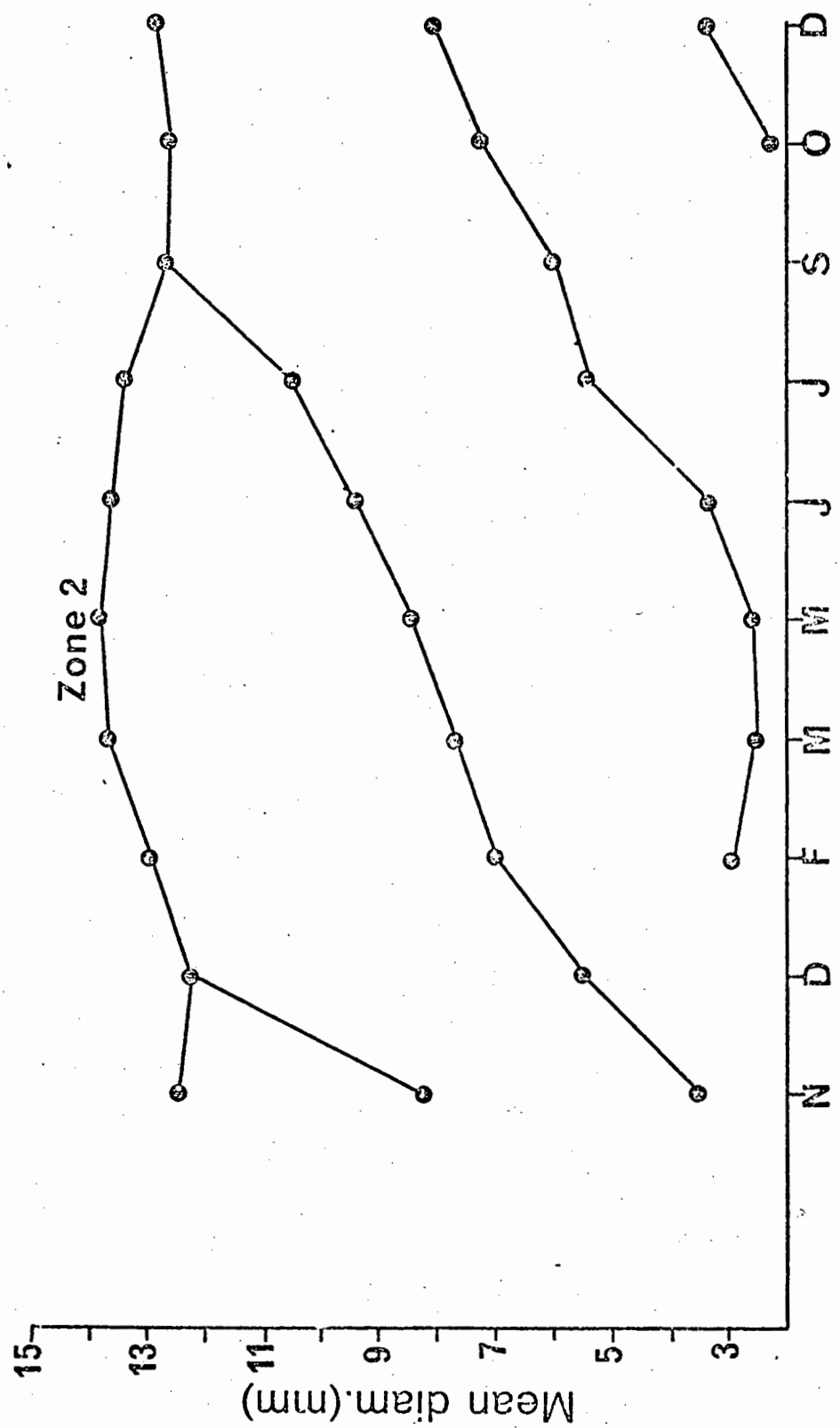


Fig. 2. 52 (Cont'd)

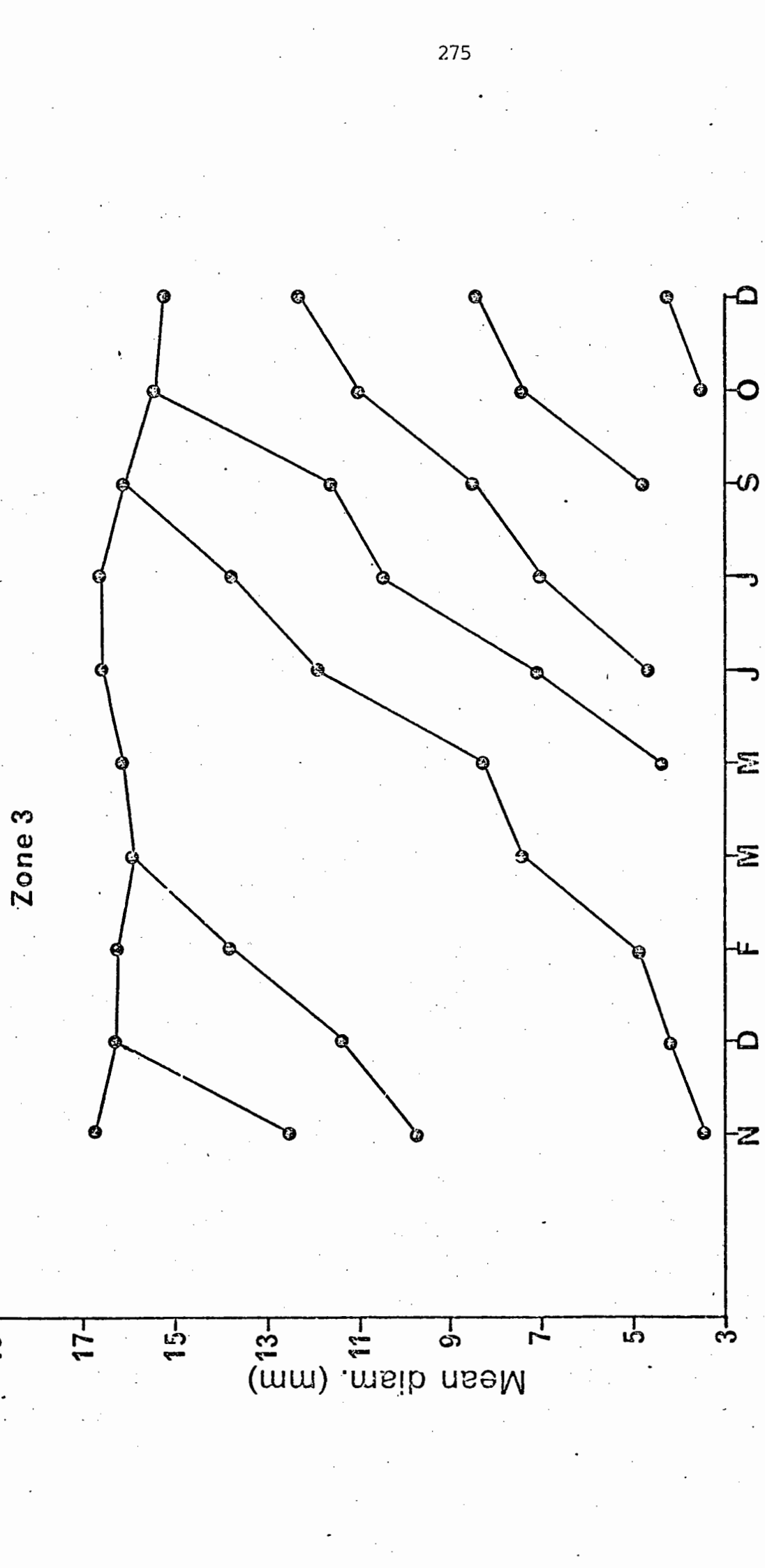


Fig. 2.52 (Cont'd)

higher density than in zone 3 (Table 2.10) and the predominance of larger animals than in zone 1 (figs. 2.32, 2.33).

There was a general decline in biomass in zones 1 and 2 due to decrease in numbers caused by migration and mortality. Although density increased greatly in February newly settled juveniles make a negligible contribution to biomass because of the exponential relationship between size and mass. Decline of biomass thus primarily reflects a decline in the number of larger animals present. There is a synchronous rise of biomass in zone 3 as biomass drops in zones 1 and 2 due to upshore migration from the lower zones. This effect is marked as medium and large sized animals are involved. A biomass decline in zone 3 after July/September 1977 may be attributed to mortality of the largest animals which are replaced by smaller immigrants from below.

4. Growth rates

Growth rates of identified cohorts in each zone are indicated as mean size versus time in fig. 2.52. Merging of cohorts in the size frequency histograms is clearly brought out here. This occurs when a younger cohort merges with an older one and results in a lowered mean size for the combined cohort (eg. in zone 1 between March and May). Similar patterns of decrease in mean size due to merging of cohorts have also been found by Underwood (1975 (a)).

The oldest cohort in zone 3 grew slowly but in zones 1 and 2 the oldest cohort often slowly declined in mean size due to emigration of the largest animals. Similarly newly settled cohorts can exhibit a decline in mean size due to prolonged recruitment of juveniles over several months (eg. zone 2 between February and May).

Growth curves for the youngest cohorts are all roughly parallel in each zone and are steepest in zones 1 and 3 indicating more rapid growth here. Thus growth rates were higher where density was lowest (c.f. Table 2.10). The ratio of primary productivity divided by mean biomass of O. variegata in each zone (data from Table 2.8 and fig. 2.51) gives an index of competition; low values indicating higher competition. This index is lower for zone 2 (16,8) than zones 1 (31,9) and 3 (25,4). Greater competition for food in zone 2 thus leads to low growth rates.

Where there is no interference by merging of cohorts the curves are sigmoidal with most rapid growth between about 5 mm and 14 mm. No animals of < 2 mm were recorded during the entire sampling period suggesting rapid growth from settlement to 2 mm. Animals reach approximately 14 mm in their first year. Growth after this is slow and extrapolation from the oldest cohort in zone 3 suggests that animals reach a size of around 18 mm after approximately 2 years. Animals of 20 mm are probably 3-4 years old or individuals showing particularly high initial growth rates.

The population is thus characterised by continuous migration of growing animals upshore from the lowest zone where settlement is heaviest. The population shows a different age structure in each zone and may be defined as:

Zone 1 Dominated by juveniles during settlement along with a small residual, presumably breeding population of about 1 year old.

Zone 2 Largely animals of 1 year old or over. A few juveniles appear during settlement but recruitment is largely due to immigration from zone 1. Very few animals remain for longer than 1,5 years (ie. > 16 mm).

Zone 3 Mainly animals of 1,5-2 or 3 years. Very few juveniles settle in this zone and recruitment is almost entirely due to migration from the lower zones.

5. Productivity

Productivity may be estimated from data on numbers and mean size in separate cohorts using the Allen curve method. Smoothed regressions of mean size and mortality against time were calculated and smoothed Allen curves derived by plotting mean number $.m^{-2}$ against mean mass for each cohort (Shafir, 1978). Productivity is given by the area under the Allen curve.

In the case of Littorina africana knysnaensis (chapter 6) this was not possible as the irregular nature of recruitment prevented the recognition of separate cohorts. Likewise for O. variegata extended recruitment into juvenile cohorts and merging of cohorts create difficulties. The numbers in cohorts can increase despite mortality (eg.

fig. 2.50,cohort C) and mean size can decrease despite growth (eg. fig. 2.52, zone 1). In addition adult cohorts often exhibit a decrease in mean size due to mortality of the oldest animals (eg. fig. 2.52, zone 3).

However regressions of mean size and of numbers against time (fig. 2.54) may be calculated for cohorts A and B in fig. 2.50 for periods of 7 and 5 months respectively (Dec. 1976 - July 1977 and February - July 1977). Data on numbers were based on fig. 2.50 and plotted on a log scale. Growth rates were derived from the growth curves generated for these two cohorts using the NORMSEP programme (fig. 2.53) and converted to changes in acidised dry mass.

Mean standing crop and mean monthly production are given in Table 2.11. Turnover was calculated as production ÷ mean biomass for the same period. Production was calculated from fig. 2.55.

TABLE 2.11: ESTIMATED MONTHLY PRODUCTION FOR COHORTS A AND B

(calculated from data for Dec. 1976-July 1977 and Feb.-July 1977 respectively).

Cohort	mean standing crop ($mg\ .m^{-2}$)	mean monthly production ($mg\ .m^{-2}$)	turnover ($\frac{P}{B}$)
A	4170,58	313,48	0,0752
B	440,56	199,34	0,4525

Net Productivity is defined (Edmondson and Winberg, 1970; Shafir, 1978) as the energy produced as an increase in body mass (Pg) plus reproductive energy (Pr). The mean diameter/weight conversion factor used for O. variegata was based on animals collected in April, when settlement rates were very low and most of the animals were spent. The production figure derived above is therefore the Pg fraction of net productivity as information on energy loss through reproduction is not included. Gross productivity may be derived as net productivity plus respired energy (Engelmann, 1966). Although data on respiration rates are not included here they have been calculated for the same population by King (1974).

The rate of production is determined largely by the rate of

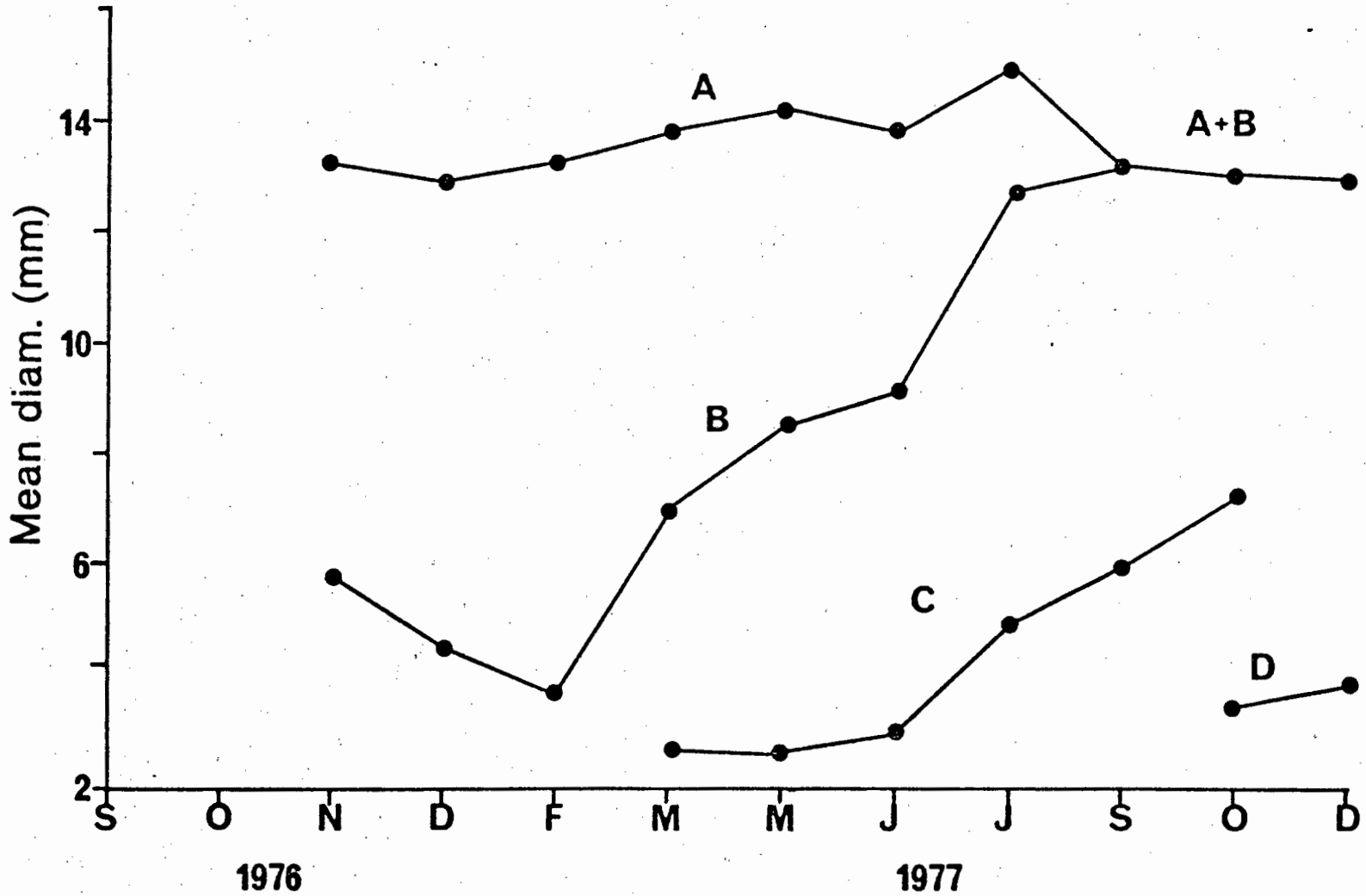


Fig. 2. 53 Composite growth curves for cohorts derived for total population of Oxystele variegata, based on fig. 2.30.

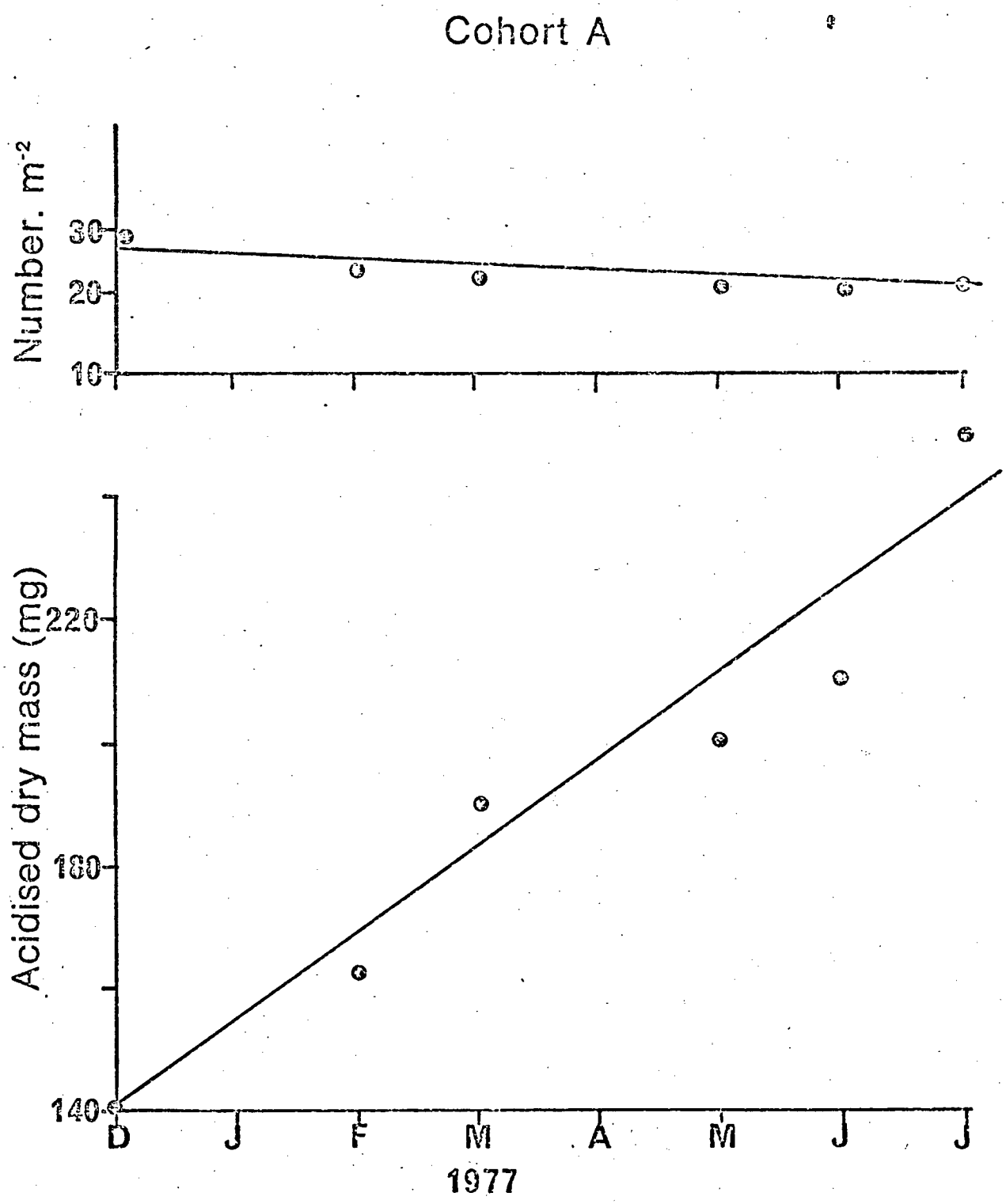


Fig. 2.54 : Increase in mean acidised dry mass (1) and decrease in numbers (2) against time for cohorts A and B identified in fig. 2.30. (Equations for mass/time regressions are:
Cohort A $y = 120,93 + 20,54\ x$ ($r = 0,92$)
Cohort B $y = 44,80 + 30,48\ x$ ($r = 0,88$))

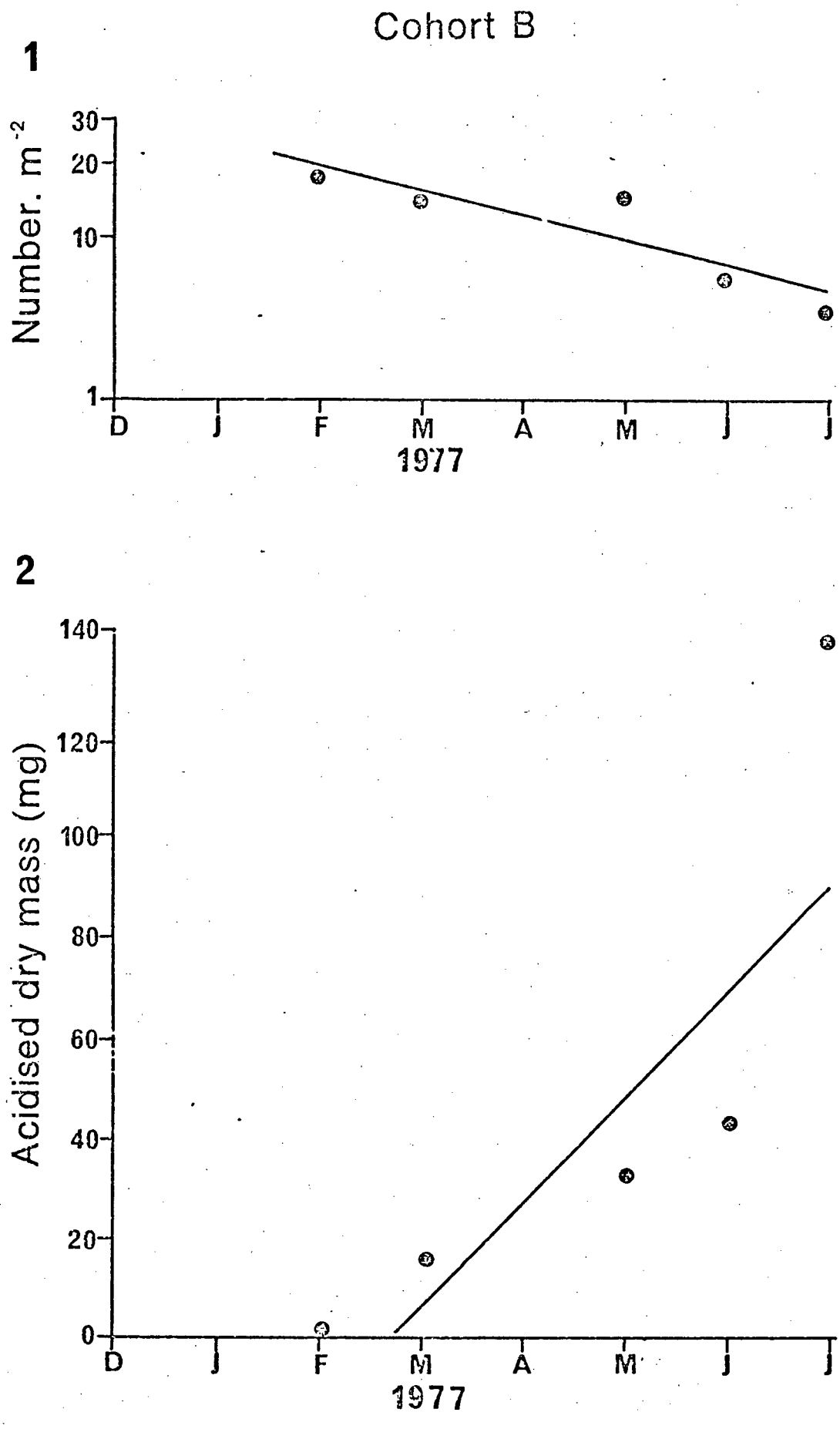


Fig. 2.54 (Cont'd)

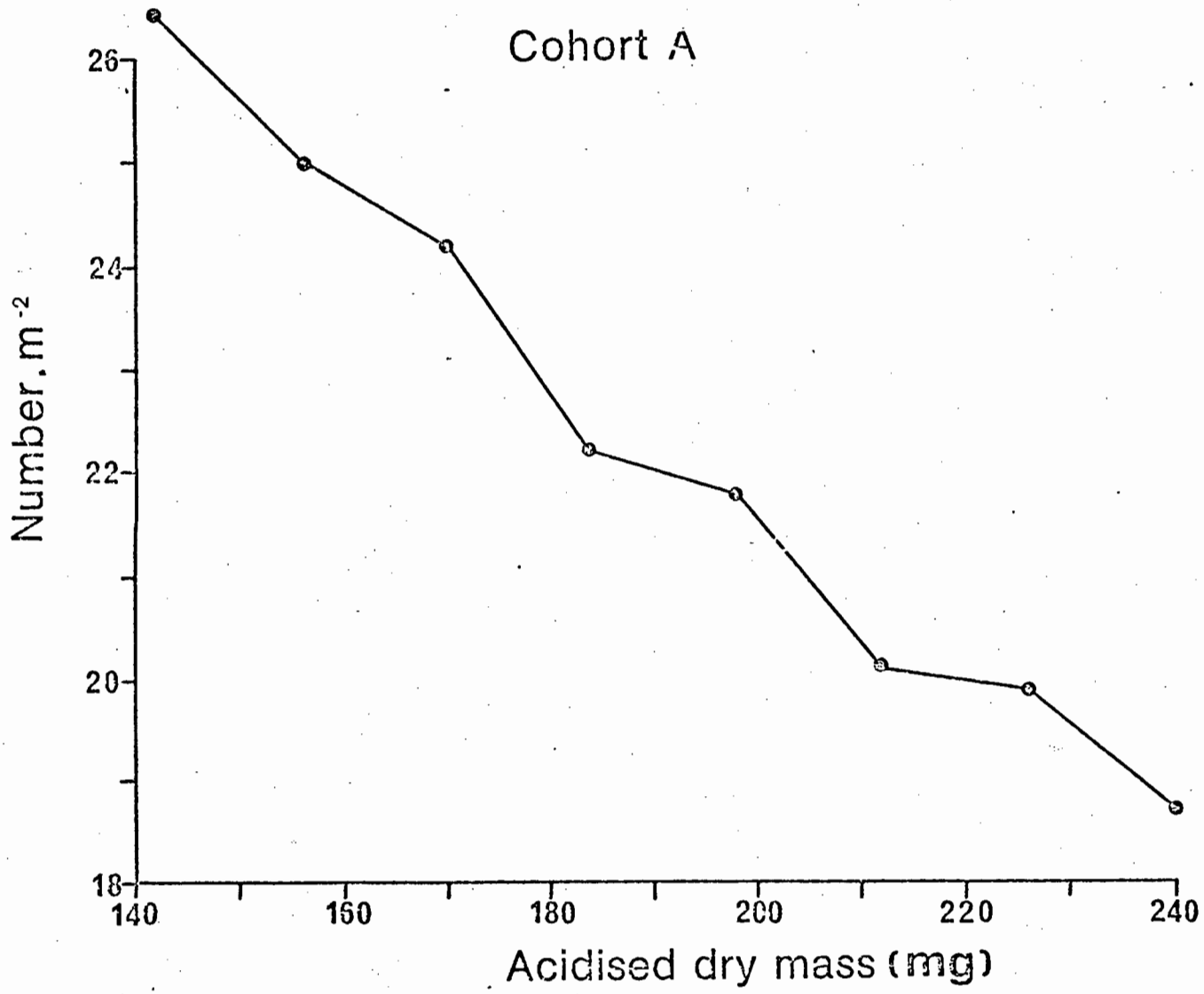


Fig. 2.55 Allen curves derived for cohorts A and B using data from figs. 2..54 A, B.

(Origins of the axes are omitted for presentation in the figure for cohort A).

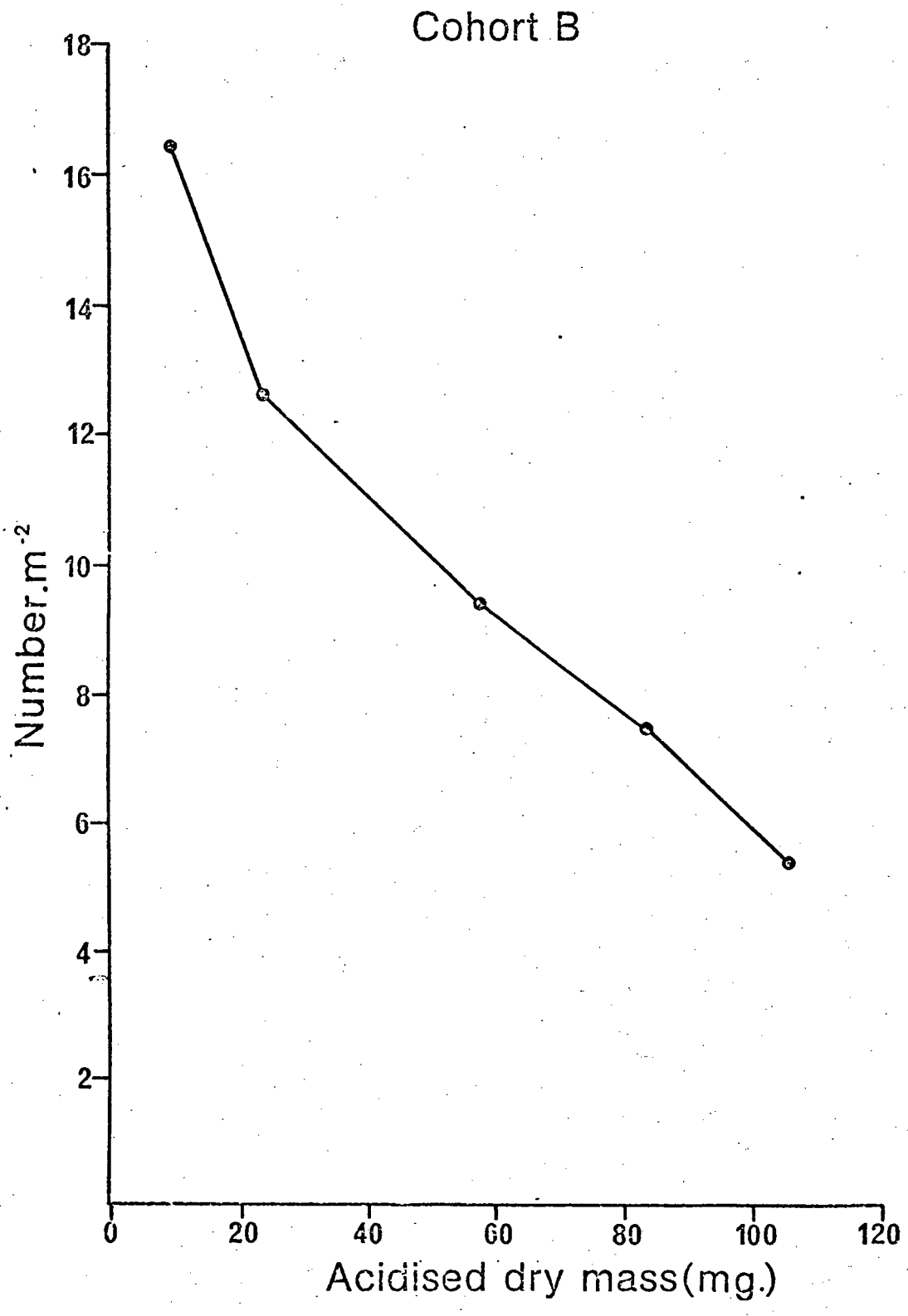


Fig. 2. 55 (Cont'd)

body growth which decreases with size. It is important to realise therefore that although mean monthly production for this period is higher for cohort A, turnover ($\frac{Pg}{biomass}$) is considerably greater for the smaller more rapidly growing animals of cohort B (Table 2.11).

Although Allen curves may not be derived for the rest of the sampling period, mean size for the combined cohort A + B was found to decline after September 1977 (fig. 2.53) due to mortality of the largest animals. Numbers also declined (fig. 2.50) and net productivity during this period would therefore be negative, reflecting a declining population (fig. 2.49).

DISCUSSION

As with Littorina africana knysnaensis (Chap. 6) O. variegata exhibits continuous reproduction, but with more marked seasonal maxima (fig. 2.30), and vertical migration leading to a size dependent zonation. Again it is necessary to consider separately the causes and implications of this zonation, patterns of settlement and growth, and of changes in the total population.

Zonation

O. variegata shows a marked size gradient at Dalebrook. Mean size was found to increase in an upshore direction, the largest animals never occurring below the upper balanoid where juveniles were extremely rare. Zones 1-3 were consequently dominated by small, medium and large animals respectively (figs. 2.31-2.33). Numbers and density were both found to be highest in zone 2 (Tables 2.9, 2.10)where the majority of animals were medium sized. There is therefore no apparent correlation between size and density.

Size dependent zonation of trochids has been described by Bakker (1959), Paine (1969), Connell (1972) and Vermeij (1972). Again as with L. a. knysnaensis, O. variegata does not conform to the patterns of zonation reviewed by Vermeij (1972). Despite being a mid/lower shore species O. variegata exhibits a pronounced increase in size farther upshore. This was also found for the mid-shore species Gibbula umbilicalis by Bakker (1959). Distribution based on size has been ascribed to size dependent mortality due to increased resistance with age to factors such as osmotic stress or desiccation (Coombs, 1973; Chow, 1975), the effects of wave or wind action (Behrens, 1972; Walsby, 1977), size dependent predation (Chow, 1975) or the availability of suitable crevices (Emson and Faller-Fritsch, 1976; Raffaelli, 1978; Raffaelli and Hughes, 1978).

In the case of O. variegata the size zonation exhibited may be explained more simply by a pronounced decrease in settlement higher up the shore, so that the majority of juveniles appear in zone 1, and upshore migration of animals as they grow older. This is exactly the reverse of Paine's (1969) findings for Tegula funebralis which settles

at the top of the shore and undergoes age-dependent migration down the shore. The restriction of juveniles to the lower regions may be attributed to high rates of desiccation in the upper zones. A large opercular surface area and circumference relative to body volume (fig. 2.41) leads to very rapid rates of water loss among juveniles (fig. 2.42). This, in combination with a low tolerance to desiccation in small animals (fig. 2.43) results in much higher mortality than among adults under conditions of low humidity (figs. 2.44 and 2.45). Consequently juveniles which are released in the upper balanoid move rapidly down-shore (figs. 2.35 and 2.37) and quickly die if caged in this zone (fig. 2.40). Likewise reduced physical stress and higher food availability in zone 1 result in a significantly higher body weight for adults in this zone (figs. 2.38 and 2.39). If not protected by cages however, tethered animals are preyed upon by Burnupena delalandii much more rapidly than on the upper shore (figs. 2.47 and 2.48). Although tethering causes abnormally high predation rates, natural rates must also be so high as to outweigh the advantages of life on the lower shore, as adults placed in zone 1 return very rapidly to their normal zone higher up the shore (figs. 2.34 and 2.36). An upshore shift in zonation of limpets as an avoidance response to predatory starfish has been recorded by Phillips (1976) but this is a short term effect and involves a relatively slight vertical displacement. Upshore migration would presumably normally be a gradual process as increasing resistance to desiccation allows growing animals to penetrate higher and higher upshore. For example juveniles which occur in zone 2, where algae are very sparse and conditions are dry, are restricted to narrow crevices and the tests of dead barnacles (c.f. Moyse and Nelson-Smith, 1963; Reimer, 1976). Migration from zone 1 to zone 2 may thus be a response to predation pressure. Competition in zone 2 is severe however leading to low growth rates (see above). This in turn is avoided by further migration upshore to zone 3 (where competition decreases) as the resistance to desiccation of the growing animals increases. Unlike some other intertidal gastropods O. variegata undergoes migration only on an age dependent basis and seasonal vertical migrations do not occur (c.f. Desai, 1966; Nelson-Smith, 1967; Lambert and Farley, 1968; Micallef, 1970; Underwood, 1973).

Settlement and growth

Reproduction of O. variegata appears to be continuous as small numbers of juveniles were present throughout the sampling period (fig. 2.30). There was however a very marked seasonal peak of recruitment in summer (February, 1977), when the number of juveniles increased enormously (fig. 2.30), with less distinct periods of increased settlement in winter (May/June) and spring (October). Seasonal recruitment has been found for other species of trochids by E.E. Williams (1964b), Desai, (1966), Paine (1969, 1971(b)) and Regis (1969).

Settlement (that is successful settlement or the number of juveniles surviving to 2 mm) occurred primarily in the lower zones and the number of juveniles decreased markedly from zone 1 to zone 3 (figs. 2.31-2.33). Despite intensive collection and examination of algal scrapings from lower down the shore O. variegata was never recorded below zone 1 and, as with L. a. knysnaensis, subtidal settlement followed by upshore migration may be excluded (c.f. Smith and Newell, 1955). Settlement must therefore be followed by very rapid growth (c.f. Berry, 1961) as animals of less than 2 mm were rare and no animals of less than 1 mm were recorded. Growth from 2 mm was sigmoidal, being most rapid during the first year after settlement, from 5 mm to 14 mm (fig. 2.52). Growth then declined to low rates, possibly due to the onset of sexual maturity combined with lower food availability in the zones occupied by larger animals.

Growth rates were highest in zones 1 and 3 and lower rates in zone 2 are due to the high density there (Table 2.10) leading to more severe competition for food (c.f. Underwood, 1976). Data for zone 3 however are based on the occurrence of very low numbers of juveniles (fig. 2.33) and it may be assumed that young animals grow most rapidly in zone 1 where settlement was heaviest. Again this may also be related to the availability of food in each zone and increased environmental stress up the shore.

Mortality and Numerical changes

Normal life span appears to be 2 years (around 18 mm) although animals of 20 mm or over may be much older (c.f. Comfort, 1957; Darby,

1964; Paine, 1969). This is in agreement with the observed adult mortality rate of approximately 4,08 % per month. Numbers of juveniles declined in zones 1 and 2 after settlement in February 1977 due to a combination of high juvenile mortality and migration up the shore (fig. 2.49). In zone 3 however there were few juveniles present and numbers increased towards the end of the sampling period. This increase reflects both migration, as juveniles from the February settlement grew larger and migrated upshore, and the lower mortality of adults, which form the bulk of this sub-population. These numerical changes are mirrored by biomass changes in each zone (fig. 2.51) which showed a decline in zones 1 and 2 and a gradual increase in zone 3 towards the end of the sampling period. There was however a decline in biomass in zone 3 after July 1977 despite an increase in actual numbers (c.f. figs. 2.51, 2.49). This was due to mortality of the largest animals and their replacement by larger numbers of smaller animals migrating up the shore.

From fig. 2.50 it can be seen that the combined cohort formed by merging of the adult and juvenile cohorts A and B in September 1977 remained smaller than cohort A had been in November 1976. In addition the winter and spring periods of settlement (May and October 1977) involved only very limited recruitment (fig. 2.30) and did not lead to an increase in total population (fig. 2.49). Thus mortality during the sampling period outstripped recruitment and total population showed an overall decline of 31 % from December 1976 to December 1977. This was in direct contrast to the increase in population of Littorina africana knysnaensis over the same period (see Chap. 6).

This decline is attributable largely to very high rates of juvenile mortality. Even a large number of juveniles make a relatively small contribution to total biomass. However juveniles are important not simply in terms of maintaining overall population size but also because they show a high turnover rate (Table 2.11) and may therefore play an important part in energy flow through the population as a whole.

Although O. variegata is abundant throughout the balanoid zone, vertical size gradients and zone dependent densities imply differential grazing pressure in different regions of the beach. The

influence of high densities of O. variegata on algal biomass in the mid balanoid has been described above (Chap. 5) and it is indicative of the complexity of the system that the gradients exhibited by O. variegata are themselves maintained in part by predation by Burnupena delalandii.

SUMMARY

1. Size dependent zonation of Oxystele variegata occurs, shell size increasing in an upshore direction. This is caused by higher settlement rates at the bottom of the shore, the upper shore offering conditions too severe for juveniles, particularly in terms of desiccation. Juveniles suffer rapid water loss due to a relatively large opercular surface area and have a low resistance to desiccation. This leads to high mortality under reduced humidities. As animals increase in size their resistance to desiccation increases allowing them to migrate upshore. This is a response to high rates of predation in the lower zones. Predation is, in fact, so intense as to override the advantages of higher food availability and more equable physical conditions on the lower shore.

2. The existence of a size gradient has a distinct influence on biomass in each zone. Density is also zone dependent and consequently the impact of the species as a grazer may be expected to vary in different zones.

3. Settlement was continuous but with a very marked peak of recruitment in summer. Growth is most rapid for the first year after settlement (up to approximately 14 mm) and then declines. Growth of juveniles was lower in zone 2 than in zones 1 and 3, because of the higher density and more severe competition for food there. A normal lifespan of 2 years (approximately 18 mm) is implied but animals of up to 22 mm may be older.

4. Monthly mortality of adults was found to be 4,08 % and that of juveniles 12,44 %. The population of O. variegata at Dalebrook was found to decrease by 30,80 % over a period of 13 months. Decrease in numbers occurred only on the lower shore (zones 1 and 2) and was related to high juvenile mortality rates.

5. Mean monthly somatic production (Pg) was calculated for one juvenile and one adult cohort for 5 and 7 months respectively. Although adult production was higher, turnover (ie. the $\frac{P}{B}$ ratio) was much greater for juvenile animals.

CHAPTER 8 : SYNTHESIS

In this study an attempt has been made to define spatial and temporal variations in rocky intertidal communities in the Cape Peninsula, South Africa and to examine the causes and significance of these variations. There is a great diversity of beach types in this area characterised by specific types of intertidal communities and the communities are themselves very heterogenous.

The classic patterns of zonation defined by Stephenson and Stephenson (1949) apply well to these beaches with the proviso that they form a simplification of actual conditions. The major zones are generally obvious and on some beaches they form sequential bands up the shore. On most beaches however they form a complex mosaic of zones, and position across the shore is an important consideration in the use of transects. These zones may of course be subdivided into an infinite number of sub-zones but a certain degree of division into sub-communities, defined by species dominance, is essential if species biomass for the beach as a whole is to be accurately assessed.

The cause of vertical zonation has in the past, been attributed to the occurrence of "critical tidal levels" on the shore where submersion/emersion ratios change suddenly and dramatically (eg. Colman, 1933; Doty, 1946; Evans, R.G. 1957; Lewis, 1964). More recently however this has been contested by Underwood (1978) who suggests that the causes of zonation vary for each species. These causes probably include factors such as food availability (eg. Underwood, 1972b) and biotic interactions such as active orientation of some species towards the presence of others (Williams, G.B. 1964; Newell, 1979) or predation (including grazing) and competition (eg. Connell, 1961a, b, 1972; Paine, 1971, Chapman, 1973; Haven, 1973; Menge, 1976). The effects of tidal rise and fall are obviously still of considerable importance, operating through modifications of temperature and particularly desiccation extremes at different heights up the beach. For example both total biomass and species richness decrease towards the supralittoral fringe, the latter probably due to both a reduction in the number of niche types available and increased physical stress (Newell, 1979).

Communities may be defined by species composition and biomass. These two parameters were found to be controlled primarily by sea temperature and the degree of wave exposure respectively. Temperature has a zoogeographic influence on species distribution (eg. Isaac, 1937; Stephenson, 1944; Lewis, 1964; Brown and Jarman, 1978) and results in a framework of species presence on the warm and cold coasts of the Cape Peninsula. This framework is modified by the occurrence of ubiquitous species and overlap of the west and south coast biota as described by Stephenson (1944) and confirmed on a quantitative basis in the present study.

Both warm and cold coast beaches have a similar pattern of trophic compartment biomass distribution up the shore. The biomass of the trophic compartments considered was found to be generally dominated by one or only a few species and approximately 90 % of total biomass on the twelve beaches examined was formed by a total of only 45 species. Biomass of many of these species was strongly influenced by the degree of exposure leading to different patterns of trophic biomass on exposed and sheltered beaches. The majority of species influenced by the degree of wave action favour more exposed conditions, which is indicative of the generally exposed nature of the whole coastline. Consequently total biomass was found to be significantly higher on exposed beaches as was biomass of filter-feeders, omnivores and carnivores. Filter-feeders in particular are of great importance and tend to dominate trophic biomass on exposed shores. As the actual species composition of the trophic compartments was largely determined by the influence of temperature, subdivision of beach types into warm exposed, cold exposed etc. is necessary. Patterns of energy-flow through the intertidal community may however be expected to differ at a fundamental level on exposed and sheltered shores and further data on the major species described may be expected to give a good insight into these patterns.

The basic pattern of community types established by temperature and exposure effects is locally modified by unstable or easily eroded substrate conditions which have an impoverishing influence on the biota, especially sedentary forms. Local offshore currents may also influence the biota by affecting settlement rates.

Important effects caused by biotic interactions can also alter community structure. For example, it was found that the lower shore is structured largely under the influence of Patella cochlear which can attain very high densities and, through grazing, causes important changes in species richness and algal biomass in the cochlear zone.

Having considered spatial variation in these communities it is essential to realise that important temporal changes also occur. Both algal and gastropod populations were found to show seasonal variations overlain by long-term effects.

The algal community examined consisted of three elements corresponding to the canopy, understorey and fugitive components described by Dayton (1975). These were termed dominant species and subdominant species (which were not necessarily canopy or understorey species respectively) with the opportunistic dominant Ulva sp. fulfilling the role of a fugitive species. Both zonation and biomass changes occurred, the structure of the community as a whole being dictated primarily by the response of dominants to variations in physical conditions and of the subdominants and Ulva sp. to competition with these dominant species. The most important physical factor examined was the height of diurnal low tides and biomass of all dominant species showed a high correlation with these tidal conditions. Their biomass was greatest in summer during periods of increased height of low tides. This may have been due largely to increased photosynthetic rates caused by greater depth and duration of submergence.

The height of extreme low tides does not follow a strictly seasonal pattern each year however and during the winter of 1979 low tides were particularly high. Although quantitative samples were not taken, the biomass of dominant algae was obviously much higher than in previous winters. Similarly during the summer of 1979 tidal heights were low and algal biomass appeared lower than in preceding years. It appears that although algal standing crop fluctuates primarily in response to the effects of tidal factors these effects are augmented if favourable tides occur during the summer. Algal biomass is thus influenced by the interplay of tidal factors with the more regular seasonal changes in light intensity and temperature.

Dominant species produced up to 100 % cover in most zones and the out-competed subdominants showed higher biomass during periods of dominant recession. Competition between dominant species was avoided by clear dominance of one or two species in each zone. Where two dominant species occurred in a single zone their biomass peaked in different months each year. Low tides were markedly higher in 1976 than in 1977 and dominant species reached much higher biomass in this year while sub-dominants showed the reverse. The exception to this was Ulva sp. which was most common in the middle shore where Gelidium pristoides was dominant. Biomass of Ulva sp. exhibited the same pattern as sub-dominant biomass, exploiting the recession of G. pristoides between 1976 and 1977. Although grazing is largely responsible for community structuring in the cochlear zone and may be severe in the case of some balanoid algal species, high algal biomass and growth rates swamp the influence of herbivores during most of the year. Grazing effects are probably most important during periods of low algal biomass and would affect absolute biomass levels rather than influencing seasonal patterns of abundance.

During periods of increased algal standing crop the biomass of dominant species increased initially at the bottom of the shore where conditions suitable for rapid growth, especially increased submersion effects, became effective first. This was followed after several months by upshore extension of range during periods of high biomass. It is generally accepted that the upper limits of intertidal algal distribution are set by the ability of each species to withstand increased desiccation and light intensity up the shore, the lower limits being controlled by biotic interactions such as competition (Connell, 1972; Chapman, 1973). Spreading of species into higher zones may therefore be seen as a response to improved upshore physical conditions. In the case of sub-dominants however it may also have been largely an exploitation of the decrease in competition caused by dominant recession. Gigartina radula and Centroceras clavulatum also extended their range downshore as their biomass increased, the latter in response to a drop in dominant biomass on the lower shore during winter. Downshore extension of the dominant species G. radula during peak biomass was possible because of its large size and rapid growth, allowing it to compete strongly for both light and space.

Calorific content, considered on an ash free dry weight basis, was found to show a seasonal cycle related to biomass changes and was maximal during periods of rapid growth. This corresponds to periods when the protein : carbohydrate/fat ratio may be expected to be low. Biomass fluctuations were so great that they form the main influence on algal standing crop considered as KJ $.m^{-2}$. Seasonal change in the calorific value of algae does however affect the quality of food available to macrophytic herbivores and may in certain circumstances have an important influence on herbivore/algal relationships. For example a seasonal drop in the energy content of food species may be compensated for by a greater intake by herbivores and thus increased grazing pressure.

The populations of two species of prosobranch gastropods studied also showed seasonal and long term changes as well as spatial variation. Both species showed a marked vertical size gradient, the length of Littorina africana knysnaensis decreasing and maximum diameter of Oxystele variegata increasing up the shore. There was no correlation between density and size gradients, the latter being the reverse of those which would be predicted by Vermeij's (1972) generalised model. Vermeij (1972) has attributed size gradients of intertidal molluscs to physical stress at the top of the shore and predation or other biotic effects on the lower shore. In the cases examined the gradients were caused by restriction of the juveniles to certain zones by physical effects (wave action in the case of L. a. knysnaensis and desiccation in the case of O. variegata). These zones were sub-optimal for biotic reasons (food availability or predation) and the greater physical resilience of adults allowed them to migrate to the more favourable zones from which juveniles were physically excluded, resulting in a vertical size gradient.

Both populations may be subdivided into three "subpopulations" which were not physically isolated from one another but occupied different zones on the shore.

1. The first subpopulation occurred in the zone of juvenile recruitment where settlement rates were highest. No large animals and few medium sized animals were found in this zone. This subpopulation occupied the bottom of the beach in the case of O. variegata and the uppermost zone in the case of L.a. knysnaensis.

2. The middle subpopulation was intermediate in both cases, consisting of medium sized animals with few large individuals. Settlement also occurred in this zone but was more limited and much recruitment was due to migration of growing juveniles from the first zone.

3. The upper subpopulation of O. variegata and the lowest subpopulation of L. a. knysnaensis represented adult zones where the animals were largest. There was very limited successful settlement here and recruitment was mainly due to migration from the middle zone.

As may be expected numbers decreased from the first to the last zone although this did not always correlate with a decrease in density as the zones were of varying sizes.

Reproduction was continuous in both species with seasonal periods of peak settlement. O. variegata exhibited a distinct summer peak of recruitment with much smaller juvenile cohorts appearing in winter and spring. Summer and winter periods of increased settlement were less obvious for L.a. knysnaensis and extended over several months. O. variegata and L. a. knysnaensis also exhibited a non-seasonal long term decline and increase in population respectively. Settlement of L. a. knysnaensis increased dramatically in 1977 and lead to very rapid growth of the population. In the case of O. variegata population decline was due to high juvenile mortality rates in 1976 so that recruitment rates were not sufficient to maintain the population. Although total population declined the adult subpopulation at the top of the balanoid zone actually increased in numbers during this period. This was caused by migration from the lower subpopulation.

Pelagic larval development with settlement at close to 1 mm seems likely for these two species and must be followed by very rapid growth as very few animals of less than 2 mm were recorded. Growth thereafter was sigmoidal and low growth rates of older animals lead to rapid merging of age cohorts, particularly in the L. a. knysnaensis population. For O. variegata growth of newly settled individuals was lower where density was high, probably because of increased competition for food. Growth and mortality rates both suggest a normal life span of 2,5 - 3 years for L. a. knysnaensis and 2 years for O. variegata.

CONCLUSIONS

This study was originally initiated as a base-line study of intertidal communities in the Cape Peninsula, as part of a long term study of the energetics of these communities. Although the study is by no means definitive three major conclusions may be drawn.

1. Intertidal communities present an overwhelming array of species occurring at different biomass in different zones. However an indication of their trophic structure and thus of the main patterns of energy flow to be expected may be drawn on the basis of the degree of exposure experienced at each beach.

   Within this trophic framework actual species composition differs on the west and east coasts of the Peninsula. Approximately 90 % of total biomass on each beach may be defined by considering the ten species showing highest biomass although other less abundant species may obviously fulfil important roles in the structure of the community.

2. Correlations exist between the biomass of dominant algal species at Dalebrook and seasonal as well as long term variations in the height of diurnal extreme low tides. This may allow the prediction of periods of high dominant species biomass, and conversely low subdominant biomass, from tidal data. Seasonal changes occur in the calorific content of the species examined and may affect algal/herbivore interactions.

3. Gastropod populations show extreme population fluctuations on a non-seasonal basis. These may be related to settlement success and temporal/spatial variations in the microflora. These populations also exhibit marked vertical size gradients due to the restriction of different size classes to zones where conditions are optimal due to either abiotic factors, in the case of juveniles, or biotic factors, in the case of adults.

A study such as this must of course be limited by the vast nature of the subject and work on three major points would be useful to consolidate these conclusions.

a) Although attention has been paid to the importance of Patella cochlear in structuring low shore communities much more work is required on the significance of biotic interactions to the patterns of community types outlined. Particularly profitable fields of study may include the effects of grazing by turbinid and limpet populations and the relationship between carnivore and filter-feeder populations.

b) Longer term study is required to confirm the correlations observed between algal biomass and tidal conditions and elucidate the effects of the interplay of tidal factors with light and temperature fluctuations. In addition it would be of interest to further examine the relationship between photosynthetic rates and depth of submergence and to confirm the existence of seasonal changes in the chemical composition of the major intertidal algal species.

c) The long term population fluctuations exhibited by gastropods may be important in terms of grazing intensity. Information on the reproduction and feeding of Oxystele variegata and Littorina africana knysnaensis and of seasonal variations in microfloral standing crop would be especially useful.

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Finally I would like to thank my family who, though far away, helped without knowing it.

APPENDIX 1 (Cont'd)

List number	Species name	Trophic compartments
24	G. pristoides	P
25	*Gigartina radula	P
26	G. scabiosa	P
27	G. stiriata	P
28	Grateloupia filicina	P
29	Gymnogongrous dilatatus	P
30	Herposiphonia sp.	P
31	Hildebrandia sp.	P
32	Hymenena venosa	P
296	Hypnea spicifera	P
33	Iridea capensis	P
34	Jania sp.	P
35	Laurencia flexuosa	P
36	L. glomorata	P
37	Pachymenia carnosa	P
38	Plocamium corralorhiza	P
39	P. cornutum	P
40	P. suhrii	P
41	Polysiphonia incompta	P
42	Porphyra capensis	P
43	Pterosiphonia cloiophylla	P
286	Ralfsia expansa	P
44	Sargassum heterophyllum	P
45	Splachnidium rugosum	P
46	Streblocladia corymbifera	P
47	Ulva sp.	P
	Porifera	
48	Hymeniacedon perlevis	F
	Actiniaria-hydrozoa	
49	Kirchenpaueria pinnata	C
	-Anthozoa	
50	Actinia equina	C
51	Anthothoe stimpsoni	C
52	Bunodactis reynaudi	C
53	Bunodosoma capensis	C
54	Pseudactinia flagellifera	C

* In an addendum to Simons (1976) key to algal species recently produced (March 1979) Gigartina radula is replaced by G. hystrix which may in fact be a species complex.

APPENDIX 1 (Cont'd)

List number	Species name	Trophic compartments
	Stauromedusae	
55	Haliclystis sp.	C
	Platyhelminthes	
56	Notoplana patellarum	C
57	Polyclad sp.	C
	Nemertea	
58	Amphiporus sp.	C
59	Cerebratulus fuscus	C
60	Lineus olivaceous	C
278	L. ornatus	C
61	L. sp.	C
62	Nemertean sp.	C
63	Zygonemertes capensis	C
	Sipunculida	
304	Golfingia capensis	D
64	Themiste minor	D
65	T. stephensoni	D
	Nematoda	
274	Nematode spp.	D
	Polychaeta-errantia	
66	Arabella iricolor cauerlea	C
67	Bhwania gcodei	C
68	Eulalia capensis	C
69	Eunice capensis	C
70	Euphrosine capensis	C
283	Exogone clavator	C
71	Exogone verugera	C
72	Glycera tridactyla	C
266	Lepidonotus semitectus	C
73	L. cavifrons	C
74	Lumbrinereis coccinea	C
267	L. tetraura	C
75	Lysidice natalensis	O
76	Morphysa capensis	C
77	M. depressa	C
290	M. sanguinea	D
78	Marphysa sp.	D

APPENDIX 1 (Cont'd)

list number	Species name	Trophic compartments
79	Nereis operata	O
284	N. sp.	O
80	N. willeyi	O
81	Paronuphis antartica	C
82	Perinereis nuntia vallata	C
83	P. capensis	C
280	Platynereis calodonta	C
84	Platynereis dumerillii	H
85	Pseudonereis variegata	O
86	Syllis armillaris	C
279	Syllis sp. 1 (c.f. S.amica)	C
294	Syllis sp. 2	C
87	Syllis sp. 3	C
88	S. variegata	C
	-Sedentaria	
89	Amphiglena mediterranea	F
90	Branchiomma natalensis	F
303	B. violacea	F
91	Cirriformia capensis	D
92	Cirriformia sp.	D
93	C. tentaculata	D
94	Dodecaceria pulchra	F
95	Gunnarea capensis	F
96	Loimia medusa	D
97	Megalomma quadrioculatum	F
98	Naineris laevigata	D
99	Nicolea macrobranchia	D
100	Orbinid sp.	D
101	Orbinia angrapequensis	D
102	Pherusa laevis	D
103	Polydora sp.	D
104	P. capensis	D
105	Pomatoleios Kraussi	F
106	Potamilla reniformis	F
281	Sabella penicillus	F
107	Sabellastarte longa	F
300	Scoloplos johnstonei	D
108	Serpulid sp.	F

APPENDIX 1 (Cont'd)

List number	Species name	Trophic compartments
109	Terebella pterochaeta	D
110	Terebellid sp. 1	D
111	Terebellid sp. 2	D
112	Thelepus cornatus	F
113	Thelepus sp.	F
299	Vermiliopsis glandigerous	F
	-Oligochaeta	
277	Oligochaeta sp.	D
	Crustacea-Cirripedia	
114	Balanus algicola	F
115	B. maxillaris	F
116	Chthalamus dentatus	F
117	Octomeris angulosa	F
118	Tetraclita serrata	F
	-Isopoda	
119	Cirolana rugicauda	C
120	C. incisicauda	C
287	C. venusticauda	C
121	Cymodocella pustulata	S
122	C. sublevis	S
123	Dynamenella australis	S
124	D. dioxus	S
125	D. huttoni	S
308	D. macrocephala	S
126	D. ovalis	S
127	D. scabricula	S
128	D. sp.	S
129	Exosphaeroma antikraussi	S
130	E. kraussi	S
131	E. laeviusculum	S
132	E. planum	S
133	E. porrectum	S
134	Exosphaeroma sp.	S
135	E. truncatitelson	S
136	E. varicolor	S
137	Iais pubescens	S
138	Glyptidotea lichtensteni	S
103	Jaeropsis sp.	D
139	Janiropsis palpalis	D
140	Mesanthura catenula	C

APPENDIX 1 (Cont'd)

List number	Species Name	Trophic compartments.
276	Niambia sp.	D
141	Paridotea facicola	H
142	P. rubra	H
143	P. ungulata	H
144	Parisocladus perforatus	S
145	P. stimpsoni	S
146	Sphaeramene polytylotos	S
147	Stenetrium sp.	D
	-Amphipoda	
148	Amaryllis macropthalma	D
149	Aora kergueleni	F
289	Ampelisca anomala	F
150	Ampithoe africana	F
151	A. falsa	F
152	A. ramondi	F
153	Ampelisca diadema	F
154	Aristias symbiotica	S
155	Calliopiella michaelseni	S
156	Caprellina longicolis	C
157	Caprella natalensis	C
158	Ceradocus rubromaculatus	C
271	Corophium acherusicum	D
159	Elasmopus japonicus	S
291	Erichthonius brasiliensis	F
268	Eusiroides monoculoides	C
292	Gammaropsis afra	F
160	Hyale diastema	H
161	H. grandicornis	H
162	Ischyrocerus anguipes	D
273	I. gorgoniae	D
288	Jammiropsis afra	F
270	Jassa falcata	D
164	Lembos hypacanthus	F
305	Lysianassa cinghalensis	S
165	L. ceratina	S
166	L. variegata	S
167	Macrophisthopus stebbingi	S
308	Maera vagans	C

APPENDIX 1 (Cont'd)

List number	Species name	Trophic compartments
293	Melita orgasmos	C
168	Paramoera capensis	S
169	Podocerus africana	C
170	P. inconspicuus	C
307	Polycaria atolli	F
171	Stenothoe sp.	C
172	Temnophlias capensis	S
272	Talorchestia sp.	H
	-Tanaidacea	
173	Anatanais gracilis	C
174	Leptochelia barnardi	C
175	L. savignyi	C
176	Parapseudes spongicola	C
177	Tanais philetaerus	C
	-Leptostraca	
178	Nebalia capensis	S
	-Anomura	
179	Paguristes barnardi	S
180	P. gamianus	S
	-Brachyura	
181	Cyclograpsus punctatus	S
182	Dromidia hirsutissima	S
183	Pilumnoides perlatus	S
184	Plagusia chabrus	S
	-Insecta	
185	Anurida maritima	D
298	Collembola sp.	D
186	Telmatogeton minor (larvae only)	H
	Arachnida-Pycnogonida	
187	Achelia quadridentata	C
188	Tanystylum brevipes	C
	-Aranea	
189	Desis formidablis	C
	Mollusca-Amphineura	
190	Acanthochiton garnoti	H
191	Chaetopleura papilio	H
192	Chiton nigrovirescens	H

APPENDIX 1 (Cont'd)

List number	Species name	Trophic compartments
193	C. tulipa	H
194	Ischnochiton oniscus	H
	-Pelecypoda	
195	Aulacomya ater	F
196	Chlamys tinctus	F
197	Choromytilus meridionalis	F
198	Gregariella simplicifilis	F
199	Kellya rubra	F
200	Perna perna	F
201	Saxicava arctica	F
202	Tapes corrugatus	F
203	Tellina gilchristi	F
204	Thecalia concamerata	F
	-Gastropoda	
205	Afracominella elongata	C
206	Burnupena delalandii	S/C
207	B. lagenaria	S
208	B. limbosa	S
209	B. papyracea	S
210	Clavatula sinuata	C
211	Conus elongatus	C
212	Crepidula aculeata	H
213	C. porcellana	H
214	C. rugosa	H
215	Eatoniella nigra	H
216	Fasciolaria lugubris	C
217	Fissurella mutabilis	H
218	Gibbula beckeri	H
219	G. capensis	H
220	G. cicer	H
221	G. rosea	H
222	Haliotis midae	H
223	H. sanguineum	H
224	Helcion dunkeri	H
225	H. pectunculus	H
226	H. pruinosus	H
227	Littorina africana	H
228	L. knysnaensis	H

APPENDIX I (Cont'd)

List number	Species name	Trophic compartments
229	Marginella capensis	C
230	Ocenebria puncturata	H
231	Onchidella capensis	H
232	Oxystele sinensis	H
233	O. tigrina	H
234	O. variegata	H
235	Patella argenvillei	H
236	P. barbara	H
237	P. cochlear	H
238	P. granatina	H
239	P. granularis	H
240	P. longicosta	H
241	P. miniata	H
242	P. oculus	H
243	P. tabularis	H
244	Pyrene kraussi	C
245	Siphonaria aspera	H
246	S. deflexa	H
247	S. capensis	H
248	Thais cingulata	C
249	T. dubia	C
250	T. squamosa	C
251	Tricolia capensis	H
252	T. neritina	H
253	Tritonallia puncturata	C
254	Turbo sarmaticus	H
255	Turitella capensis	H
	Echinodermata-Asteroidea	
256	Henricia ornata	C
257	Patinella exigua	H
	-Ophiuroidea	
258	Amphioplus integer	D
259	Amphipholis squamata	D
260	Amphiura capensis	D
261	Parechinus angulosus	D

APPENDIX 1 (Cont'd)

List number	Species name	Trophic compartments
	-Holothuroidea	
262	Cucumaria frauenfeldii	O
263	Golfingia capensis	O
275	Pentacucumis spyridophora	O
264	Thyone aurea	O
	-Tunicata	
310	Ascidia sydneinsis	F
265	Pyura stolonifera	F

	SEAPOINT	OUDEKRAAL A	OUDEKRAAL B	ROBBEN ISLAND	OLIFANTS -BOS	KOMMET-JIE	BUFFELS BAY A	BUFFELS BAY B	FROGGY POND A	FROGGY POND B	DALEBROOK	STRAND-FONTEIN
61	.0000	.0000	.0030	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0007	.0000
62	.0268	.0000	.0560	.0000	.0023	.0000	.0176	.0000	.0000	.0000	.0007	.0000
63	.4149	.0000	.0132	.0288	.0000	.0000	.0154	.2464	.1602	.0680	.0000	.0055
64	.0000	.0000	.0000	.3232	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
65	.0000	.0000	.0000	.0000	.0000	.0000	.2571	.1420	.0000	.0000	.0000	.0000
66	.0000	.0000	.0033	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
67	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.1900	.0000
68	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
69	.0000	.0000	.0000	.0000	.0260	.0000	.0000	.0000	.0000	.0000	.0000	.0000
70	.0195	.0000	.0004	.1239	.0000	.1108	.0000	.0000	.0000	.1956	.2445	.0000
71	.0486	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0075	.0000
72	.0000	.0000	.0000	.0000	.0000	.0000	.0033	.0000	.0000	.0000	.0000	.0000
73	.0000	.0000	.0000	.0173	.0000	.0000	.0000	.0000	.7742	.1726	.2815	.2056
74	.0033	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0864	.0000	.0000	.0720
75	.0000	.0000	.0000	.0000	.4855	.1526	.2400	.2280	.5118	.0000	.2433	.4886
76	.0000	.0000	.0000	.0000	.1958	.0000	.0000	.0000	.0000	.0000	.0000	.0000
77	.1375	.0000	.1300	.0000	.0000	.0728	.0000	.0000	.0000	.0000	.0000	.0000
78	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0250	.0000
79	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	1.1800	.0000	.0000	.0000
80	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	1.9037	.0000
81	.0000	.0000	.0000	.0000	.4980	.0010	.0000	.0000	.0000	.0000	.0000	.0000
82	.0000	.0000	.0500	.0000	.1532	.0000	.0000	.0000	.0000	.0000	.0000	.0000
83	.0000	.0000	.0000	.0000	.0000	.0000	.0424	.0424	.0084	.0071	.5110	.0000
84	.5929	.0000	.7473	.0489	.3177	.4032	.3755	1.5328	1.7952	1.0570	.6630	2.8815
85	16.2995	.6050	5.6919	14.4016	.4578	.0000	1.3047	.5511	.4090	14.1663	3.7750	6.4402
86	.0007	.0000	.0000	.0655	.0000	.0066	.0000	.0000	.0237	.2767	.0237	.0021
87	.0000	.0000	.1713	.0515	.0856	.0355	.0000	.0000	.0250	.2890	.0938	.0061
88	.0649	.0000	.4401	.0097	.0034	.0700	.0039	.0022	.0248	.0556	.0649	.0178
89	.0000	.0000	.0000	.0000	.0008	.0015	.0000	.0000	.0000	.0000	.0000	.0000
90	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0912	.0000
91	.2834	.0000	.0000	.0000	.8632	.6800	.0000	.0000	1.6416	5.8533	2.3671	.2240
92	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0016	7.1227	.0000	.0000
93	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.2355	.0000
94	.0000	.1142	.1142	1.9778	.2900	.0128	.0988	.0000	.1031	.0000	.0000	.0000
95	3.5337	.2846	.0000	.0387	.6583	.3697	.0000	.0000	1.5288	.6517	1.6241	2.8792
96	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.3132	.0000
97	.0025	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	1.9266	.0000
98	.0000	.0000	.0000	.0000	.0091	.0000	.0000	.0000	.0000	.0000	.0000	.0000
99	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0072	.0000
100	.0000	.0000	.0000	.0000	.0017	.0008	.0000	.0000	.0000	.0000	.0000	.0000
101	.0000	.0000	.0000	.1088	.0000	.0030	.0000	.0000	.0000	.0000	.0000	.0000
102	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0700	.0693	.0000	.0000
103	.0000	.0000	.0007	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
104	.0000	.0000	.0075	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.3093	.0000
105	.0000	.0000	.0000	.0000	.0000	.0000	.0364	.1648	.0000	.0200	.0052	.1032
106	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	1.8419	.0000
107	.0000	.0000	.9500	.0000	.0000	.0000	.0000	.0000	.0132	.3945	.2448	.0000
108	.0000	.0000	.0000	.0000	.1651	.0000	.0000	.0000	.0000	.0000	.0000	.0000
109	.0000	.0000	.1300	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
110	.0000	.0000	.0103	.0000	.0000	.0000	.0222	.0000	.0000	.0773	.0000	.0000
111	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0773	.0000	.0000
112	.0000	.0000	.0000	.0000	.6877	.0000	.0000	.0000	.0000	.0700	.0000	.0000
113	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0640	.0000
114	.0000	.1142	1.4777	64.2620	.0000	.0000	.0000	.0324	.0000	53.3810	.0000	.5077
115	.0000	.0000	7.3387	.6000	.0000	.0000	.0000	.0000	.0000	5.0465	8.8018	1.4728
116	.0000	.0000	.0000	.0000	.0000	.0000	.1287	.0000	.0992	7.9145	.0000	.0000
117	53.3799	.0000	307.4000	395.3913	.0229	.0000	211.6960	.0000	25.1576	1640.1595	294.3545	.4693
118	8.1350	.0000	397.0000	55.3375	.0000	19.5932	35.8446	13.1661	17.2635	8.8850	585.0467	271.9800
119	.0000	.0000	.0000	.0000	.0000	1.0490	.0000	.0000	.0000	.0000	.0104	.0000
120	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.1524	.0000	.0000	.0000
121	.0088	.0000	.0000	.0000	.0007	.5922	.0000	.0000	.0012	.0000	.0024	.0000
122	.0071	.0000	.0228	.2794	.0107	.5008	.0042	.0000	.0142	.0020	.0024	.0016

	SEAPOINT	OUDEKRAAL A	OUDEKRAAL B	ROBBEN ISLAND	OLIFANTS -BOS	KOMMET-JIE	BUFFELS BAY A	BUFFELS BAY B	FROGGY POND A	FROGGY POND B	DALEBROOK	STRAND-FONTEIN
123	3.3618	.1618	.2405	2.1104	.0084	.0000	.0000	.0000	.0000	.0953	.0237	.0000
124	.0000	.0000	.0000	.0000	.0000	.0000	.0400	.0000	.0406	.0000	.0111	.1164
125	1.0033	.0328	2.3505	1.8006	1.0641	1.1491	.0526	.0566	.6357	18.4577	.8590	.1840
126	.0111	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
127	.0000	.0000	11.0000	.0000	.2092	.0048	.0699	.0000	.0000	3.4209	.0000	.0000
128	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	1.4143	.0000	.0000
129	1.3073	.0000	.0000	.0000	.0163	.3556	.0070	.0000	.0536	.0000	.0000	.0720
130	.4200	.0000	.0000	.0000	.0000	11.8380	.0000	.0000	.0000	.0000	.0328	.0000
131	.0044	.0044	.9758	.0000	.0020	1.9316	.0638	.0000	.2432	.0158	.1836	.0000
132	.0000	.0000	.0000	.0164	.0000	.9469	.0928	.1059	.1296	.0000	.0000	.0000
133	.0000	.0000	.0000	.0000	.0000	1.1308	.0000	.0000	.0000	.0000	.0000	.0450
134	.1554	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
135	.0868	.0000	.0000	.0000	.0179	.0000	.0000	.0000	.0000	.0000	.0000	.0000
136	.0000	.0000	.0000	.0120	.0044	.3708	.0000	1.3842	.6299	.0484	.1103	.0008
137	.0000	.0000	.0145	.0000	.0000	.0808	.0002	.0082	.0804	.0289	.0243	.0123
138	.0000	.0000	.0000	.0000	19.4450	.0120	.0000	.0000	.0000	.0000	.0000	.0000
139	.0013	.0000	.0178	.0026	.0000	.0040	.0000	.0000	.0000	.0000	.0000	.0034
140	.0000	.0000	.0000	.0000	.0000	.0020	.0000	.0000	.0336	.0000	.0000	.0000
141	10.2942	.0000	.0000	.0000	.0000	.0132	3.3056	.0512	.2500	.0000	.0000	.0000
142	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.2092	.0000	.0000	.0000
143	2.5900	.0000	.0000	.2683	2.0300	1.0358	.0000	.0000	.0000	.0000	.0000	.0000
144	.0000	.0076	.1378	.0000	.0000	.3577	.0243	1.0044	.1572	.0000	.1379	.0000
145	.0590	.1112	.2400	.0003	1.3888	.4472	.0233	.0348	.0822	.0224	.4189	1.1104
146	.0000	.0000	.0000	.0003	.0196	1.2482	.0000	.0000	.0000	.0000	.0000	.0000
147	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0064
148	.0000	.0000	.0000	.0000	.0000	.0000	.0555	.0000	.1049	.0000	.0000	.0000
149	.0000	.0000	.0000	.0000	.0266	.0000	.0000	.0000	.0164	.1243	.0056	.0384
150	.0000	.0000	.0000	.0000	.0472	.0000	.0000	.0000	.0000	.0000	.0000	.0000
151	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0371	.0000	.0000
152	.0000	.0000	.0000	.0000	.0480	.0000	.0000	.0000	.0000	.0000	.0000	.0000
153	.0000	.0000	.0000	.0000	.0326	1.8296	.0000	.0000	.0000	.0000	.0000	.0000

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154	.0000	.0000	.0000	.0000	.0000	2.0384	.0000	.0000	.0000	.0000	.0000	.0007
155	.0000	.0000	.0000	.0000	.0280	.1511	.0000	.0108	.0000	.0000	.0000	.0000
156	.0000	.0000	.0000	.0000	.0159	.0954	.0000	.0000	.0018	.0340	.0819	.0000
157	.0000	.0000	.0000	.0000	.0040	.0000	.0000	.0000	.0000	.0657	.0000	.0000
158	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0384	.0000	.0000	.0000
159	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0192	.0000	.2075	.3416
160	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0322	.7595	.4620	.3082
161	.4040	.0037	.2012	.2547	.5756	1.0456	.0844	.0680	.0000	.0000	.0000	.0000
162	.0000	.0000	.0000	.0000	.0000	.8269	.0000	.0300	.0000	.0000	.0784	.0000
163	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0004	.0036	.0000	.0000	.0000
164	.0000	.0000	.0000	.0000	.0000	.0175	.0000	.0668	.0000	.0000	.0000	.0000
165	.0119	.0000	.0139	.0490	.0274	1.5632	.0000	.0000	.5229	.2452	.3187	.0330
166	.0000	.0000	.0000	.0000	.0559	.0000	.0000	.0000	.0000	.0000	.0000	.0000
167	.2365	.0000	.0000	.0000	.0000	.0000	.0262	.0478	.0000	.0000	.0000	.0000
168	.3271	.0026	.3741	.1439	.0605	.3555	.0452	.0554	.0020	.5546	.1991	.0734
169	.0000	.0000	.0000	.0000	.0000	.0000	.1625	.0000	.0000	.0810	.0000	.0000
170	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0711	.0000	.0000	.0000
171	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.5166	.0191	.0000
172	.0000	.0000	.0187	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
173	.0000	.0000	.0000	.0113	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
174	.0000	.0000	.0000	.0004	.0000	.0960	.0299	.0064	.0088	.0414	.0496	.0237
175	.0000	.0000	.0000	.0360	.0000	.0020	.0000	.0000	.0000	.0000	.0000	.0000
176	.0000	.0000	.0000	.0000	.0000	.3000	.0652	.0000	.0000	.0000	.0000	.0000
177	.0000	.0000	.0000	.0024	.0000	.2744	.0000	.0000	.0000	.0000	.0072	.0297
178	.0000	.0000	.0000	.0000	.0000	.6406	.0000	.0000	.0000	.0000	.0000	.0000
179	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
180	.0000	.0000	.0000	.0000	.0000	.0007	.0000	.3744	.0000	.0000	.2836	.0000
181	.0000	.0000	.0000	.0000	.0000	.9000	5.3310	6.0623	.0000	.0000	.0000	.0000
182	.0000	.0000	.0000	.0000	.0000	.0000	.1944	.0000	.0000	.0000	.0000	.0000
183	.0000	.0000	.0000	.1719	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
184	.2191	.0000	.1332	.0000	.0000	.4128	1.0454	.3596	.2157	.4000	4.0594	1.2240

	SEAPOINT	OUDEKRAAL A	OUDEKRAAL B	ROBBEN ISLAND	OLIFANTS -BOS	KOMMET-JIE	BUFFELS BAY A	BUFFELS BAY B	FROGGY POND A	FROGGY POND B	DALEBROOK	STRAND-FONTEIN
185	.0000	.0000	.0000	.2047	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
186	.0369	.0000	.0228	.0048	.0008	.5744	.0156	.0233	.0349	.3148	.1230	.0589
187	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0799	.0000	.0000
188	.0000	.0000	.4138	.0000	.0000	.0969	.0000	.0000	.0288	.3251	.0000	.0000
189	.0000	.0000	.5475	.0000	.0000	.0000	.0684	.1226	.0816	.0840	.1192	.0000
190	1.4667	.0000	35.6400	.0000	.0000	.0595	1.8576	1.5385	.2322	.0000	2.1106	23.5272
191	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.1521	.0000
192	.9008	.0000	28.7630	3.8776	.0179	6.9728	2.0855	.0198	.0000	.0000	.6556	.0000
193	.0000	.0000	.0000	.2569	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
194	.0000	.0004	.0000	.0000	.0000	.0000	.0000	.0810	.0000	.0000	.0000	.0000
195	74.0670	.9746	283.7536	99.2693	.6674	.3330	1.5395	.0000	3.8153	70.8562	5.6416	9.5792
196	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.1228	.0671	.0000	.0000
197	53.5066	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.7646	1.9041	.9920	.0000
198	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0050	.0000	.0000
199	.0000	.0000	.1162	.3201	.0091	.1564	.0768	.0000	.0588	.6296	.0969	.0000
200	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.9434	27.1975	4.8127	.0000
201	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.1075	.0000	.0000
202	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	1.0296	.0000	63.8625
203	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0348	.0000	.1000	.0000
204	.0000	.0000	.0000	.0000	.0000	.0000	.8754	1.5194	.1520	.1647	.0000	.0000
205	.0000	.0000	.0000	.0000	.0000	2.2262	.0000	.0000	.0000	.0000	.0000	.0000
206	26.4666	.0000	.0000	5.9671	21.6880	4.7127	3.1410	18.3316	.3880	4.4273	6.8868	2.3282
207	.0000	.0000	.0000	.0000	.0000	.0000	1.5096	7.4040	5.5240	2.2000	.3994	14.7200
208	.0000	.0000	.0000	.0000	.0000	7.2673	1.1502	.0000	.0000	.0000	.0000	.0000
209	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	23.5400	.0000	.0000	.0000
210	.0000	.0000	.0000	.0000	.0000	.0508	.0000	.0000	.0000	.0000	.0000	.0000
211	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.2185	.0000
212	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	1.5783	.0000
213	.0000	.0000	.0000	.0000	.0833	1.0517	.0490	.0011	1.0574	.0300	.8189	.1094
214	.0417	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
215	.0000	.0000	.1013	.0175	.0178	1.2619	.3261	.0000	.1365	.2701	.1962	.1215
216	.0000	.0000	.0000	.0000	.0000	.5044	.0000	.0000	.0000	.0000	.0000	.0000
217	.9023	.0004	.3518	1.6767	.0004	1.4270	.0000	.0000	.0232	1.0192	.2535	.0096
218	1.6519	.0000	.0000	.0000	.0000	5.6539	.0000	.0000	.0000	.0000	.0000	.0000
219	.0000	.0000	.0000	3.1065	.0000	.8049	1.0494	.0164	.5056	.0000	.0000	.2868
220	.0000	.0000	.0000	.0000	.0000	.2000	.0000	.0000	.0000	.0000	.3973	.0300
221	1.5067	.0000	.0000	.0000	.0000	.0000	.0011	.0039	.0089	.0000	.0956	.7648
222	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
223	.0704	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
224	.0000	.2000	.0000	.0000	.0020	.9919	.0000	.0000	.0000	.1650	.0000	.0000
225	.0000	.0000	.0000	4.0664	3.9833	.0000	4.4879	13.0262	.0000	.0000	1.3865	.1744
226	1.5467	.0000	.0000	1.5224	.0000	.5784	.1705	.7112	.0000	.0000	.0600	.0000
227	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0280	.0000	.0000
228	1.0790	4.4534	2.9819	3.3129	4.2408	4.0832	.6908	.6908	3.0896	8.9170	8.3760	.9252
229	.0000	.0000	.0000	.2510	.0000	.0414	.0000	.0000	.0000	.0000	.0000	.0001
230	.0000	.0000	.0000	.0000	.0000	.0250	.0728	.0000	.0000	.0000	.0000	.0000
231	.0000	.0000	1.1900	.8436	.0000	.0000	.0851	.0000	.0576	2.4688	.0000	.9000
232	.0000	.0000	.0000	.0000	.0000	.0000	3.4820	4.6625	2.2400	.0000	9.2835	.3384
233	10.2000	.0000	30.8230	2.2399	.7713	.2844	1.0108	7.5456	1.7360	.0000	1.5200	.0000
234	12.0000	.0000	.0000	.0200	8.1720	1.3160	6.6271	27.8532	6.1687	9.5329	9.5779	8.8395
235	5.8353	.0000	.0000	43.8865	9.2840	.0000	.0000	.0000	.0000	7.6197	.2620	.0000
236	31.9200	.0000	.0000	.0000	14.1753	22.8600	27.6000	.0000	14.2540	30.7185	8.0847	247.0547
237	32.1731	42.5960	42.5966	136.8237	45.1683	9.1400	26.2990	51.6180	40.9333	110.8890	71.3667	.0000
238	10.0096	11.6667	8.0027	2.3555	16.4675	239.1600	4.6550	1.0400	5.8800	.0000	2.1600	.0000
239	40.3860	41.1997	30.4004	22.9928	6.9240	15.3269	8.2634	.0000	1.6800	12.1404	2.7595	15.4535
240	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	2.7120	1.9600	7.7902	1.6787
241	.0000	.0000	.0000	.0000	.0000	.0000	4.0000	.0000	.0000	.0000	2.5671	.1219
242	32.9120	.0000	.0000	.0000	.0305	18.8670	6.7217	12.1443	6.8850	.0000	16.6625	9.6000
243	.0000	2.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
244	.0000	.0000	.0000	.0000	.0092	.2445	.1264	.0208	.0344	.0000	.0000	.1218
245	1.0792	.0000	2.2000	.0000	.0100	9.9000	.3803	.0000	.2820	1.6662	1.9467	6.0299
246	.0000	43.1200	.0000	5.7634	12.0664	11.4963	2.4461	.0000	.5224	.0000	11.0910	3.4011

	SEAPOINT	OUDEKRAAL A	OUDEKRAAL B	ROBBEN ISLAND	OLIFANTS -BOS	KOMMET-JIE	BUFFELS BAY A	BUFFELS BAY B	FROGGY POND A	FROGGY POND B	DALEBROOK	STRAND-FONTEIN
247	.7420	1.4[illegible]6	.1167	3.5743	6.6422	19.9570	.0000	.0000	.0000	.0000	3.6069	5.462[illegible]
248	.0051	.01[illegible]6	3.3340	.0000	3.2164	.0000	.0000	.0000	.0000	.5484	.0000	.0000
249	.9200	.00[illegible]0	1.9489	.0000	.0000	.2975	.0000	.0000	1.0773	10.0190	4.6500	8.0754
250	.0000	.00[illegible]0	.2214	.0000	.0000	3.8566	.0000	.0000	.0000	.1813	.0000	3.6495
251	.0000	.00[illegible]0	.0000	.0000	.3993	.4897	.0033	.0033	.0182	.0000	.0232	3.2764
252	.0067	.00[illegible]0	.1216	.2529	.0659	.5904	.7803	.0009	.1406	.1414	1.1500	.0396
253	.0000	.00[illegible]0	.0000	.0000	.0008	.0008	.0190	.0000	.0000	.0000	.1948	.0009
254	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	8.8868	.0000	.0000	.0000	.0000	.0009
255	.0000	.00[illegible]0	.0000	.0000	.0000	.0122	.0000	.0000	.0000	.0000	.0000	.0000
256	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	1.9018	.0000	.0000	.0127
257	22.5465	.00[illegible]0	.0000	6.8951	.0000	.0000	.8746	1.5453	.0000	.0000	9.6085	4.4933
258	1.0323	.00[illegible]0	.0000	.8045	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
259	.4000	.00[illegible]0	.0000	.8144	.0000	.0193	.1277	.3348	.3844	.0000	.0317	.3264
260	.1648	.00[illegible]0	.0000	.0000	.0000	.0000	.0177	.0000	.0000	.0000	.0000	.0000
261	27.3239	.00[illegible]0	1.1737	25.0710	.0000	.0000	20.6960	71.7000	9.7100	.0000	158.5166	89.1269
262	.0000	.00[illegible]0	.0000	.0000	.2491	.0000	.0000	.0000	.0000	.0000	.0000	.0000
263	.1748	.00[illegible]0	.0000	.6669	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
264	.0268	.00[illegible]0	.1508	.0000	.0000	.0000	.0000	.0000	.2436	6.3936	.0000	.0000
265	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	43.3325	94.6115	1571.1200	167.5800
266	.5587	.00[illegible]0	.5451	.2173	.0000	.0000	.1977	.4852	.5574	.1984	.1789	.0000
267	.0025	.00[illegible]0	.0030	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
268	.0114	.00[illegible]0	.0000	.0000	.0009	.0000	.0000	.0000	.0000	.0000	.0000	.0000
269	.0000	.00[illegible]0	.0000	7.6020	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
270	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0085	.0000
271	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
272	.0000	.0074	.1372	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
273	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
274	.0000	.00[illegible]0	.0420	.0067	.0028	.0000	.0000	.0000	.0770	.0011	.0000	.0064
275	.0000	.00[illegible]0	.1675	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
276	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
277	.0000	.00[illegible]0	.0425	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
278	.0000	.00[illegible]0	.0224	.2800	.0036	.0000	.0000	.0000	.0000	.0000	.0000	.0000
279	.0000	.00[illegible]0	.0336	.0137	.0021	.0006	.0000	.0000	.0000	.0000	.0000	.0000
280	.0000	.00[illegible]0	.0000	.0500	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
281	.0000	.00[illegible]0	.0000	.1600	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
282	.0000	.00[illegible]0	.0000	.4640	5.8608	245.4100	.0000	.0000	.0000	.0000	.0000	.0000
283	.0000	.00[illegible]0	.0000	.0592	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
284	.0000	.00[illegible]0	.0000	.0000	.2636	.0000	.0000	.0000	.0000	.0000	.0000	.0000
285	.0000	.00[illegible]0	.0000	.0300	.0000	.0000	10.7700	.0000	.0000	.0000	.0000	.0000
286	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.2917	.0000
287	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	2.0224	.2596	.0000	.0000	.0000
288	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0040	.0000	.0000	.0000	.0000	.0000
289	.0000	.00[illegible]0	.0000	.0000	.0000	.0251	.0000	.0000	.0000	.0000	.0000	.0000
290	.0000	.00[illegible]0	.0000	.0000	.0000	.0238	.0000	.0000	.0000	.0000	.0000	.0000
291	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0052	.0000	.0000	.0000	.0000
292	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0016	.0000	.0000	.0000	.0000
293	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0157	.0000	.0000
294	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.1528	.1327	.0000
295	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	1.3738	.0000
296	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	37.1140	32.1070
297	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.2760	.0000
298	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0010	.0000	.0000	.0000	.0000	.0075
299	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0452
300	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0032
301	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	378.4000
302	.0000	.00[illegible]0	.0000	.7104	.0000	.0000	.0000	.0000	.0000	.0000	.8202	.0000
303	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.6239	.0000
304	.1748	.00[illegible]0	.0000	.0000	1.4464	.0000	.0000	.0000	.0000	.0000	.8910	.0000
305	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0315	.0000	.0000
306	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	6.1172	.0000
307	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0044	.0000	.0000
308	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0155	.0000	.0000
309	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0312	.0000	.0000
310	.0000	.00[illegible]0	.0000	.0000	.0000	.0000	.0000	.0000	8.2172	.0000	.0000	.0000

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